University of Alberta

A dendroecological investigation of inter-annual variability in growth, competition, and spatial pattern of jack pine forests

By

Juha Mikael Metsaranta

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements of the degree of *Doctor of Philosophy*

in

Forest Biology and Management

Department of Renewable Resources

Edmonton, Alberta

Spring 2008

Library and Archives Canada

Published Heritage Branch

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque et Archives Canada

Direction du Patrimoine de l'édition

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence
ISBN: 978-0-494-45566-1
Our file Notre référence
ISBN: 978-0-494-45566-1

NOTICE:
The author has granted a non-exclusive license allowing Library and Archives Canada to reproduce, publish, archive, preserve, conserve, communicate to the public by telecommunication or on the Internet, loan, distribute and sell theses worldwide, for commercial or non-commercial purposes, in microform, paper, electronic and/or any other formats.

The author retains copyright ownership and moral rights in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

AVIS:
L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, publier, archiver, sauvegarder, conserver, transmettre au public par télécommunication ou par l'Internet, prêter, distribuer et vendre des thèses partout dans le monde, à des fins commerciales ou autres, sur support microforme, papier, électronique et/ou autres formats.

L'auteur conserve la propriété du droit d'auteur et des droits moraux qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

Canada

University of Alberta

Library Release Form

Name of Author: Juha Mikael Metsaranta

Title of Thesis: A dendroecological investigation of inter-annual variability in growth, competition, and spatial pattern of jack pine forests

Degree: Doctor of Philosophy

Year this Degree Granted: 2008

Permission is hereby granted to the University of Alberta Library to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves all other publication and other rights in association with the copyright in the thesis, and except as herein before provided, neither the thesis nor any substantial portion thereof may be printed or otherwise reproduced in any material form whatsoever without the author's prior written permission.

Signature

Jun 28, 2008

Abstract

In this thesis, I studied the growth, competition and spatial pattern of mature, fire-origin, natural jack pine (*Pinus banksiana* Lamb.) forests along an ecoclimatic gradient in the boreal plains and boreal shield ecozones of Saskatchewan and Manitoba, Canada. The magnitude and causes of inter-annual variation in these processes requires further study. I used a dendroecological approach to obtain annual data on these processes, which provides more information than periodic data obtained from permanent sample plots. Understanding the magnitude and causes of inter-annual variability in these processes will be needed to adapt forest management practices to climate change effects. At each of 10 study plots, I measured and cross-dated ring widths on samples obtained from a complete census of all living and dead trees detectable at the time of sampling. I found that ring-width data at breast height could be scaled to tree level volume increment with a mean error of less than 10%, and that stand reconstructions were reliable for up to 50 years into the past in this region. I examined inter-annual variation in competition in relation to stand characteristics, disturbances, and inter-annual variation in both growth rate and growing conditions. Size and growth rate were considered independently using the Gini and Lorenz asymmetry coefficients, and concurrently with an index of competition asymmetry. Inter-annual variations in competition and growth rate were significantly related, suggesting that variation in growing conditions influences competition, a possibility that is not presently accounted for in forest growth and stand development models. I also examined temporal changes in the spatial distribution of live and dead trees, and these results did not support the hypothesis that competition always leads to spatial regularity.

Acknowledgements

I thank my co-supervisors, Dr. V. Lieffers and Dr. R. Wein, and the other member of graduate committee, Dr. J. Roland for their support and feedback. I also thank my external examiner, Dr. O. Garcia, for his feedback. In particular, I thank Dr. Lieffers, for patiently and thoroughly reviewing all of my work. Even if, at the time, I didn't always appreciate the extra work resulting from these reviews, I know that it helped to make this thesis better and will make me a better scientist in the future.

I thank the Circumpolar-Boreal Alberta grants program and the Natural Science and Engineering Research Council of Canada for financially supporting the fieldwork for this project, and Derek Bakker, Jennifer Hofman, Michael Laczek, and Theresa Mundell for assistance with said fieldwork. At various times during my graduate studies, I was personally supported by a Natural Science and Engineering Research Council of Canada scholarship, a Prairie Adaptation Research Collaborative graduate scholarship, a Province of Alberta Graduate Fellowship, and a Desmond Crossley Memorial Scholarship. I (and my lack of student loan debt) thank all of these organizations for their support.

Finally, I thank my parents, Marc and Leila Metsaranta, for reading to me and letting me play outside as a child, and particularly for encouraging me to do whatever I wanted with my life (as long as I didn't screw up). I also thank Neety Panu for encouraging me to go through this process in the first place, and then also for putting up with me during the emotional swings of graduate school (most of the time).

Table of Contents

1.0 Introduction 1
1.1 Thesis overview 2
1.2 Study area description 3
1.3 Field data collection 4
1.4 Laboratory data processing 4
1.5 Literature Cited 6
2.0 Accuracy of annual volume increment obtained by partial stem analysis, relative to full stem analysis 13
2.1 Methods 13
2.1.1 Volume increment from full stem analysis 13
2.1.2 Volume increment from partial stem analysis 14
2.1.3 Accuracy assessment 15
2.2 Results 15
2.3 Discussion 16
2.5 Literature Cited 18
3.0 Dendrochronological reconstruction of snag and downed log dynamics 24
3.1 Methods 24
3.1.1 Field and laboratory 24
3.1.2 Estimating year of death for decomposed samples 24
3.1.3 Plot mortality trajectories 25
3.1.4 Fall rate and time since falling 25
3.2 Results 26
3.2.1 Snag and downed log persistence 26
3.2.2 Accuracy of year of death estimates 26
3.2.3 Plot mortality trajectories 27
3.2.4 Fall rate and time since falling 27
3.3 Discussion 27
3.4 Conclusion 29
3.5 Literature Cited 30

4.0 Using dendrochronology to obtain data for modeling stand development: a substitute for permanent sample plots 39
4.1 Methods 40
4.1.1 Field and laboratory 40
4.1.2 Reconstructing mortality 40
4.1.3 Reconstructing volume 40
4.1.4 Reconstructing biomass 41
4.1.5 Reconstructing diameter distributions 42
4.2 Results and Discussion 43
4.2.1 Spatial and temporal distribution of mortality 43
4.2.2 Volume growth trajectories 43
4.2.3 Biomass growth trajectories 44
4.2.4 Temporal changes in diameter distributions 44
4.3 Conclusions 45
4.4 Literature Cited 46
5.0 Inequality of size and size increment in *Pinus banksiana* in relation to stand dynamics and annual growth rate 56
5.1 Methods 57
5.1.1 Field and laboratory 57
5.1.2 Determining competition 57
5.1.3 Describing inequality 58
5.1.4 Data analysis 59
5.2 Results 59
5.2.1 Size and growth rate inequality 59
5.2.2 Average competition and competition variability 60
5.2.3 Regression model results 60
5.3 Discussion 61
5.5 Literature Cited 64
6.0 Magnitude and causes of annual variation in the mode of competition in *Pinus banksiana* 72
6.1 Methods 73

6.1.1 Field and laboratory 73
6.1.2 Mode of competition 74
6.1.3 Climate data 74
6.1.4 Insect defoliation data 75
6.1.5 Annual variation in stand level growth rate 75
6.1.6 Data analysis 75
6.2 Results 76
6.3 Discussion 76
6.4 Literature Cited 79
7.0 Annual changes in the spatial distribution of *Pinus banksiana* stands: does pattern fit competition theory? 90
7.1 Methods 91
7.1.1 Field and laboratory. 91
7.1.2 Data analysis – spatial patterns 91
7.1.3 Data analysis – stand development 92
7.2 Results 93
7.2.1 Initial and final spatial pattern 93
7.2.2 Annual change in spatial pattern 93
7.2.3 Spatial pattern in relation to stand development 94
7.3 Discussion 95
7.4 Literature Cited 98
8.0 Conclusions 107
8.1 Literature Cited 111

List of Tables

Table 1.1. Summary of select ecological, site, and stand characteristics of each study plot. 10

Table 2.1. Parameter estimates and fit statistics for the height-diameter equation..... 20

Table 2.2. Parameters for Kozak's (1988) taper equation 21

Table 2.3. Parameters (b2, c1 and c2) and metric conversion factors (a1, a2, and a3) for Honer et al's (1983) standard volume equation 22

Table 2.4. Absolute and relative prediction errors of using partial stem analysis techniques to estimate the annual volume increment of jack pine, aspen and black spruce, relative to full stem analysis. Error values in bold were considered the correct estimates of the error for that method. 23

Table 3.1. Inflection points for the mortality rate and mortality acceleration trajectories at each study plot, in comparison to those from data in Kenkel et al (1997)..... 32

Table 3.2. Snag fall rate and average, median, and 80th percentile of the standing time of snags at each study plot..... 33

Table 5.1. Parameter estimates, standard errors and p-values for the regression model for inequality of size and size increment. Parameters in bold were significant at $\alpha<0.05$. The variables are in the table are stand density (DENS), mean tree volume (SIZE), average amount of competition each tree is subject to (COMP), where competition is calculated using a distance weighted absolute size index, and stand level annual volume increment in the current year (AVI), and one year previously (AVI1). 67

Table 6.1. Description of the variables included in the 13 models evaluated by their ability to describe annual changes in competitive symmetry. All models contain age and density, and further variation is described by substituting combinations of variables related to growth rate, spring temperature, growing precipitation, drought, and occurrence of jackpine budworm. 83

Table 6.2. A ranking of the 13 apriori models described in Table 6.1, tested by their ability to describe annual changes in the index of competitive symmetry at each of the study plots. Models with an AIC ratio of less than 2 are indicated in bold. 84

Table 6.3. Regression coefficients for model 2 from Table 6.1, which was the most generally supported for describing annual changes in the index of competitive symmetry at the ten jack pine plots in this study. This model predicted the index of competition symmetry as a function of age (AGE), density (DENS), and annual volume growth rate (AVI). 85

List of Figures

Figure 1.1. The location of the study plots. The Prince Albert and Candle Lake sites are located in the Boreal Plains ecozone. The Flin Flon, Thompson, and Jenpeg sites are located in the Boreal shield ecozone. 11

Figure 1.2. Climate normals at each study region based on data from 1970 to 2000. The bars represent mean precipitation by month. The upper dark line is the mean maximum monthly temperature, and the lower dark line is the mean minimum monthly temperature. 12

Figure 3.1. Age at death, years since death, and year of death for downed logs (upper charts) and snags (lower charts). Black fill indicates trees for which the year of death was estimated from the 6 trees closest in size. Light grey fill indicates trees where year of death was determined by cross-dating the sample. 34

Figure 3.2. The relationship between measured year of death and estimated year of death for trees where year of death was known. Filled circles are snags and empty circles are downed logs. Dashed line is the line of agreement and solid line is the best-fitting linear regression line for all trees. 35

Figure 3.3. The Richards function fit to the cumulative mortality data at each study plot 36

Figure 3.4. Mortality rate (solid line) and acceleration (dashed line) trajectories for each plot based on the 2nd and 3rd derivatives of the Richards function. 37

Figure 3.5. Time since falling and year of falling of downed logs. Black areas are trees for which the year of death was estimated from 6 trees closest in size. Light grey areas are trees for which the year of death was directly measured on the samples. 38

Figure 4.2. On the left are the patterns of growth for the rich site at Candle Lake, determined from full stand reconstruction. On the right is what would be known about these patterns if a PSP had been established at the site in 1950 and re-measured every 10 years. The growth series plotted include (a) incremental volume growth (gross and net), (b) cumulative volume growth (gross and net), and (c) volume mortality (incremental and cumulative). 52

Figure 4.3. Trajectories of stemwood biomass (tonnes ha^{-1}) in living trees, standing snags, and downed logs at the rich site at Candle Lake, calculated from a complete ring-width reconstruction of all living and dead trees, using biomass equations, estimates of the fall down rate of snags, and estimates of the decomposition rate of downed logs. 53

Figure 4.4. A series of decadal histograms of the diameter distribution since 1960 for the rich site at Candle Lake, based on diameter data obtained from a complete ring-width reconstruction of all living and dead trees. The solid line represents the Weibull distribution, fit to the diameter data in each depicted year. 54

Figure 4.5. Annual trajectories of the location (a), scale (b), and shape (c) parameters of the Weibull distribution, fit to diameter distribution data each year since 1950 for the rich site at Candle Lake, based on diameter data obtained from a complete ring-width reconstruction of all living and dead trees. 55

Figure 5.1. Annual trajectories of the Gini coefficient for cumulative volume and volume increment since 1950 at each 900 m^2 study plot. The solid line represents the Gini coefficient, the dashed lines are 95% confidence intervals calculated from 1000 bootstrap samples..... 68

Figure 5.2. Annual trajectories of the Lorenz asymmetry coefficient for cumulative volume and volume increment since 1950 at each 900 m^2 study plot. The straight line indicates the value one, where the Lorenz curve is symmetric. The solid line represents the Lorenz asymmetry coefficient, the dashed lines are 95% confidence intervals calculated from 1000 bootstrap samples..... 69

Figure 5.3. Annual trajectories of the average amount of competition each tree is subject to (solid line) and the coefficient variation (CV%) of competition each tree is subject to (dashed line) at each study plot. Competition was quantified using a distance-weighted absolute size index (Eq 5.1), with a variable search radius defined as 3.5x each tree's crown width. 70

Figure 5.4. Relationship between the inequality of annual volume increment, as quantified by the Gini coefficient, and annual volume increment..... 71

Figure 6.1. Plot of the proportional growth of each tree in year t+1 against the proportional size of each tree in year t and how it is used as index of competitive symmetry. The slope of the regression line indicates relative size symmetry of growth: (a) slope=1, competition is relatively size symmetric, (b) slope>1, competition is positively size asymmetric, and (c) slope<1, competition is negatively size asymmetric.86

Figure 6.2. A demonstration of how the competition symmetry index is calculated, using data at six time decadal intervals from the poor site at Thompson. Volume and volume increment were both transformed to centered-log ratios. The thick line is the best fitting regression line. The thin line is the line of equality, indicating symmetric competition. 87

Figure 6.3. Annual trajectories of the index of competitive symmetry index (± SE) since 1950 at each study plot. An index value of one indicates symmetric competition, a value greater than one positive asymmetric competition (large trees grow disproportionately more), and a value less than one negative asymmetric competition (small trees grow disproportionately more). Dashed lines indicate periods of defoliation at each site. 88

Figure 6.4. Relationship between the annual growth rate and the index of competitive symmetry at each plot, when each is expressed as the change from year Y-1 to year Y. Significant ($p<0.05$) relationships are plotted..... 89

Figure 7.1. Initial and final locations of live (filled circles) and dead (open circles) trees at each study plot. 101

Figure 7.2. Plots of the L(t) function for living trees in 1950 and 2004 at each study plot along with 99% confidence envelope for distances of t=0 to 10 m for the hypothesis of complete spatial randomness. L(t) values above the confidence envelope indicate clustering, and L(t) values below the confidence envelope indicate regularity..... 102

Figure 7.3. Plots of the $L_{12}(t)$ function in 1960 and 2004 at each study plot along with 99% confidence envelope for distances of t=0 to 10 m for the hypothesis of random labeling of live and dead trees. $L_{12}(t)$ values above the confidence envelope indicate clustering relative to the distribution of all trees , and $L_{12}(t)$ values below the confidence envelope indicate regularity relative to the distribution of all trees..... 103

Figure 7.4. Significance of L(t) over time at each site. Time (years) is plotted along the y-axis, and distance from t=0 to 10 m in 0.1 m increments is plotted along the x-axis. Light areas indicate significant clustering, grey areas represent randomness, and dark areas indicate significant regularity. 104

Figure 7.5. Significance of $L_{12}(t)$ over time at each site. Time (years) is plotted along the y-axis, and distance from t=0 to 10 m in 0.1 m increments is plotted along the x-axis. Light areas indicate significant clustering relative to all trees, grey areas represent randomness, and dark areas indicate significant regularity relative to all trees..... 105

Figure 7.6. Temporal trajectory of mean tree spacing at each site. Time (years) is plotted on the y-axis and mean spacing of live trees (m) on the x-axis. The solid horizontal line represents the approximate time at which the spatial distribution of live trees changes from clustered to random at each site, based on Figure 7.4..... 106

1.0 Introduction

Dendroecology is the application of tree-ring analysis to scientific questions in ecology (Fritts and Swetnam 1989, Swetnam et al 1999). In this thesis, I used a dendroecological approach to examine growth, competition, and spatial pattern in jack pine (*Pinus banksiana* Lamb.) forests in the boreal plains and boreal shield ecozones in Saskatchewan and Manitoba, Canada. The magnitude and causes of inter-annual variation in these processes requires further study. Understanding the magnitude and causes of inter-annual variation in these processes is important because climate change is expected to impact the ecological structure and function of boreal forests in Canada (e.g. Hogg and Bernier 2005). Understanding this variability will be required in order to adapt management practices to climate change effects (e.g. Spittlehouse 2005). Adapting strategic planning (Harvey et al 2003) will require a further understanding of the magnitude and causes of inter-annual variation in growth, while adapting tactical planning (Andison 2003) will require further understanding of the magnitude and causes of inter-annual variation in competition processes.

In the past, data monitoring forest growth and stand development annually has been lacking. For this thesis, I obtained annual data on these processes using dendroecological stand reconstruction methods. The basic data used in most studies of boreal forests are presently obtained by periodic re-measurement of the diameter, height, and condition of trees at permanent sample plots (PSPs). Sampling designs vary by jurisdiction, but re-measurements are typically made only at 5 to 10 year intervals. This makes it difficult to use PSP data to determine the magnitude and causes of inter-annual variability. Even if undertaken, yearly re-measurement of PSPs cannot obtain annual data because instruments like tapes, calipers, and clinometers that are used to make field measurements of diameter and height have difficulty resolving the small annual growth increments typical of boreal forests. Dendroecological techniques can overcome many of these weaknesses. Ring widths measured on increment cores can be resolved annually and can provide detailed time series of growth decades into the past without waiting for PSPs to be re-measured. These measurements, combined with cross-dated patterns of past mortality and maps of the locations of living and dead trees, can reconstruct growth and stand development annually (e.g. Henry and Swan 1974, Oliver and Stephens 1976, Johnson and Fryer 1989, Stoll et al 1994, Carrer and Urbinati 2001). These data are intensive to collect, but have two desirable properties: they follow the growth of individuals over time (Weiner 1995) and they are at an annual resolution.

In plant populations, competition for depletable resources (e.g. nutrients, water) is considered symmetric. Plants obtain these resources in proportion to their size. Competition for pre-emptable resources (e.g. light) is considered asymmetric. Larger (taller) plants obtain these resources disproportionately to their size (Weiner and Thomas 1986, Weiner 1990, Schwinning and Weiner 1998). Asymmetric competition is usually considered one-sided, where large plants influence the growth of small plants, but small plants do not have any effect on large plants. Symmetric competition is usually two-sided, where small plants also have some degree of effect on large plants. In reality, the mode of competition falls somewhere on a continuum between these two extremes (Schwinning and Weiner 1998), and it is known that in even-aged tree populations, both

one-sided and two-sided competition occur (Brand and Magnussen 1988). As a result, most studies evaluate the relative size symmetry of growth (Weiner 1990, Schwinning and Weiner 1998). In any case, inter-annual variation in the importance of these different modes of competition may occur in response to transient factors like disturbance and variation in growing conditions (Weiner and Thomas 1986, Schwinning and Weiner 1998, Wichmann 2001). Two transient factors that are particularly important in this study area are insect defoliation (e.g. Volney 1988, Volney 1998) and drought (e.g. Hogg et al 2005, Hogg and Wein 2005). The magnitude of these annual variations in the mode of competition and their effects on stand development requires further study (Schwinning and Weiner 1998).

Previous studies have noted that variation in precipitation has different effects on trees of different size classes (Liu and Muller 1993, Vose and Swank 1994, Abrams and Mostoller 1995, Biondi 1996, van der Brakel and Visser 1996, Orwig and Abrams 1997, Piutti and Cescatti 1997, Wichmann 2001, Makinen et al 2002), suggesting that water availability may have an influence on stand development by its effect on inter annual variation in the mode of competition. Periodic defoliation may also influence stand development. The impacts of defoliation are a complex function of the size, number, and palatability of neighbours (Augner et al 1997), and are also dependent on whether it affects some size classes disproportionately. These impacts have not been extensively studied. Several metrics are used by plant ecologists to make inferences about changes in competition processes. Examples of these are the coefficient of skewness, the coefficient of variation, the Gini coefficient, the Lorenz asymmetry coefficient, and the distribution modifying function (Westoby 1982, Weiner and Solbrig 1984, Bendel et al 1989, Schwinning and Weiner 1998, Damgaard and Weiner 2000, Nord-Larsen et al 2006). Few studies have assessed the magnitude and causes of inter-annual variability in these metrics. The combined impact of competition and other density dependent factors, in combination with factors like drought, insect defoliation, or root rot may also impact how spatial patterns change over time. Several studies have investigated the spatial patterns of jack pine in both pure (e.g. Kenkel 1988, Kenkel et al 1997) and mixed (e.g. Little 2002, Béland et al 2003) stands, based either upon snapshots measurements of a single point in time, or periodically obtained PSP data. At this time, no other studies have used annual stand reconstruction data to assess temporal changes in spatial patterns.

1.1 Thesis overview

This thesis is subdivided into two sections. In the first (chapters 2 to 4), I focused on validating and describing the stand reconstruction methods that I used to obtain annual data on growth and stand development at my study sites. I did this by:

1) determining the accuracy of the methods that I used to scale tree-ring widths at breast height to tree level volume increment (chapter 2),

2) assessing the dynamics of snags and downed logs in order to determine how far back in time tree-ring reconstruction can reliably reconstruct these forests (chapter 3), and

3) demonstrating how tree-ring reconstruction techniques are potentially an improvement upon the permanent sample plot (PSP) data that are presently used to monitor forest growth and stand development in Canada (chapter 4).

In the second (chapters 5 to 7), I examined three aspects of the competition dynamics of these forests. These included:

1) how annual changes in the inequality of size and size increment relate to changes in stand characteristics and annual growth rate and therefore, how these factors influence the development of size hierarchies (chapter 5),

2) how annual variation in growth rate, drought, and insect defoliation affect annual changes in competitive symmetry over time(chapter 6), and

3) an examination of the spatial pattern of live and dead trees in order to determine the relative importance of competition and other factors on annual changes in these patterns during different periods of stand development (chapter 7).

1.2 Study area description

I established study plots in fire-origin jack pine stands located in the boreal plains and boreal shield ecozones (Ecological Stratification Working Group 1996) in Saskatchewan and Manitoba, Canada (Figure 1.1). The study sites were in five regions, located near (i) Prince Albert, Saskatchewan, (ii) Candle Lake, SK, (iii) Flin Flon, Manitoba, (iv) Jenpeg, MB, and (v) Thompson, MB (Figure 1.1). The Prince Albert and Candle Lake sites were in the Boreal Plains ecozone. The Flin Flon, Thompson, and Jenpeg sites were in the Boreal shield ecozone. The boreal shield landscape consists of uplands and lowlands with many bedrock outcrops. This contrasts with the boreal plains landscape, which is topographically level to gently rolling, consisting of lacustrine, aeolian or organic parent materials. Other major tree species include black spruce (*Picea mariana*), white spruce (*Picea glauca*), tamarack (*Larix laricina*), trembling aspen (*Populus tremuloides*), and white birch (*Betula papyrifera*).

Jack pine growth has been shown to be sensitive to site specific variation in weather (Larsen and MacDonald 1995, Brooks et al 1998, Hofgaard et al 1999) and to regional variation in climate and soils (McKenney and Pedlar 2003). Jack pine forests are also subject to defoliation by jack pine budworm (*Choristoneura pinus pinus* Freeman) on about a ten year cycle (Volney 1988), which influences both mortality and growth rate (Gross 1992, Volney 1998). From north to south, the study regions follow a gradient of decreasing precipitation and increasing temperature (Figure 1.2). Historical records of the Canadian Forest Insect and Disease Survey indicate that there is also a gradient of disturbance frequency in this region, with generally more recorded outbreaks of budworm in the south than in the north. As a result of these gradients, a variety of factors potentially influence the pattern of inter-annual variation in growth and dynamics of jack pine across the study area.

1.3 Field data collection

I sampled a total of 10 plots, two in each of the five regions. At each region, one plot was established at a mesic (relatively nutrient rich) site, and one plot at a xeric (relatively nutrient poor) site. I determined relative richness on the basis of ecological classification and indicator species (Beckingham et al 1996, Zoladeski et al 1995). At Candle Lake and Thompson, I established 900m^2 (30m x 30m) stem mapped plots in 2005. For these plots, the last year of growth observed was 2004. At Prince Albert, Flin Flon, and Jenpeg, I established 100 m^2 (10m x 10m) plots in 2006. For these plots, the last year of growth observed was 2005. The 100 m^2 plots were not mapped, otherwise the sampling method was the same. A full census was made of live trees, snags, and downed logs. Height was measured for living trees, breast height diameter for all living and dead trees. Two randomly oriented breast height cores were extracted from living trees and a cross-sectional disc cut from dead trees (both snags and downed logs). In addition to the breast height core sample, some trees at each site (n=25 at 900 m^2 plots, n=10 at 100 m2 plots) were cored at ground level in order to determine an estimate of the age of the stand. At all plots, the samples collected represent a complete census of all live or dead trees present in the stand at the time of sampling. The characteristics of each of the study plots are summarized in Table 1.1.

1.4 Laboratory data processing

I air dried the samples, mounted the cores on grooved boards and cut the cross-sectional discs into 1-2 cm thick slices. I then polished them with up to 600 grit sandpaper and scanned them as 1600 dpi grey scale images. Ring widths were measured on these images with the WinDendro (Regent Instruments, Quebec, Canada) analysis system. Under growth suppression, jack pine tends to form very light rings (Volney and Mallett 1992) that were not always visible on the scanned images. I further examined these samples using a microscope so that rings not visible on the scanned image could be identified and added to the WinDendro file. In cases of extreme suppression (< 5% of samples), the year of death was potentially underestimated if the tree continued to live for several years after radial growth ceased at breast height. As in Mast and Veblen (1994), trees were considered functionally dead when radial growth ceased at breast height. Only a single tree out of n=1070 living and dead trees measured in this study showed evidence of recovery (defined as resumption of measurable radial growth) from such extreme suppression.

I developed a master chronology from 25 (in the case of 900 m^2 plots) or 10 (in the case of 100 m^2 plots) of the largest trees for each site. Jack pine forests in this region are regularly defoliated by the jack pine budworm (*Choristoneura pinus pinus* Freeman) (Volney 1988). I cross-dated the samples visually against the master chronology by reference to narrow marker years (Yamaguchi 1991) induced by this defoliation. Dating was quantitatively checked using a procedure that assessed the correlation between the raw ring widths on a sample and the raw ring widths on the site master chronology, as well as shifting the dates of the sample 1 to 5 years forward or backwards. This was done iteratively until most living (82%) and dead (76%) samples had the highest correlation at the final assigned date (91% for the final assigned data ±1 year for living trees, 90% for

dead trees). Samples had high visual correspondence between marker years on the sample and the site master chronology at the final assigned date, though the correlation may have been slightly higher at slightly shifted dates. The average correlation between a dead sample and the master chronology at the final assigned date was R^2=0.88 (SD=0.09, range=0.76 to 0.99, n=429). For living trees, it was R^2=0.81 (SD=0.19, range=0.58 to 0.99, n=536). No dead trees showed evidence of having persisted from the stand prior to the last stand replacing disturbance. The study sites were even-aged, so the breast height age only ranged over a small interval (around 5 years), so visual cross-dating was sufficient to confidently date each dead sample. The quantitative tests were used only to identify gross errors in the initial dating.

1.5 Literature Cited

Abrams, M.D., and S.A. Mostoller. 1995. Gas exchange, leaf structure, and nitrogen in contrasting successional tree species growing in open and understory sites during a drought. Tree Physiology 15:361-370.

Andison, D.W. 2003. Tactical forest planning and landscape design. *In* Burton, P.J., C. Messier, D.W. Smith, and W.L. Adamowicz, (eds.).Towards Sustainable Management of the Boreal Forest.pp.433-480.NRC Research Press, Ottawa, ON.

Augner, M., J. Tuomi, and M. Rousi. 1997. Effects of defoliation on competitive interactions in European white birch. Ecology 78:2369-2377.

Beckingham, J.D., D.G. Neilsen, and V.A. Futoransky. 1996. Field guide to the ecosites of the mid-boreal ecoregions of Saskatchewan. Nat.Res.Can., Can.For.Serv., North.For.Cent., Edmonton, AB. Spec.Rep.6.

Béland, M., J-M. Lussier, Y. Bergeron, M-H. Longpre, and M. Béland. 2003. Structure, spatial distribution and competition in mixed jack pine (*Pinus banksiana*) stand on clay soils of eastern Canada. Ann.For.Sci. 60:609-617.

Bendel, R.B., S.S. Higgins, J.E. Teberg, and D.A. Pyke. 1989. Comparison of skewness coefficient, coefficient of variation, and Gini coefficient as inequality measures within populations. Oecologia 78:394-400.

Biondi, F. 1996. Decadal-scale dynamics at the Gus Pearson Natural Area: evidence for inverse (a)symmetric competition? Can.J.For.Res. 26: 1397-1406.

Brand, D.G., and S. Magnussen. 1988. Asymmetric, two-sided competion in even aged monocultures of red pine. Can.J.For.Res. 18:901-910.

Brooks, J.R., L.B. Flanagan, and J.R. Ehrlinger. 1998. Responses of boreal conifers to climate fluctuations: indications from tree-ring widths and carbon isotope analyses. Can.J.For.Res. 28:524-533

Carrer, M., and C. Urbinati. 2001. Spatial analysis of structural and tree-ring related parameters in a timberline forest in the Italian Alps. J.Veg.Sci. 12:643-52.

Damgaard, C. and J. Weiner. 2000. Describing inequality in plant size or fecundity. Ecology 81:1139-1142

Ecological Stratification Working Group. 1996. A National Ecological Framework for Canada. Agriculture and Agri-Food Canada, Research Branch, Centre for Land and Biological Resources Research and Environment Canada, State of Environment Directorate, Ottawa, ON. 125 pp.

Fritts, H.C., and T.W. Swetnam. 1989. Dendroecology: A tool for evaluating variations in past and present forest environments. Adv.Ecol.Res.19:111-188.

Gross, H.L. 1992. Impact analysis for a jack pine budworm infestation in Ontario. Can.J.For.Res. 22:818-831.

Harvey, B.D., T. Nguyen-Xuan, Y. Bergeron, S. Gauthier, and L. Leduc. 2003. Forest management planning based on natural disturbance and forest dynamics. *In* Burton, P.J., C. Messier, D.W. Smith, and W.L. Adamowicz, (eds.).Towards Sustainable Management of the Boreal Forest.pp.395-432. NRC Research Press, Ottawa, ON.

Henry, J.D., and J.M.A. Swan. 1974. Reconstructing forest history from live and dead plant material – an approach to the study of forest succession in southwest New Hampshire. Ecology 55:772-783.

Hofgaard, A. J. Tardif, and Y. Bergeron. 1999. Dendroclimatic response of *Picea mariana* and *Pinus banksiana* along a latitudinal gradient in the eastern Canadian boreal forest. Can.J.For.Res. 29:1333-1346.

Hogg, E.H., J.P. Brandt, and B. Kochtubajda. 2005. Factors affecting interannual variation in growth of western Canadian aspen forests during 1951-2000. Can.J.For.Res. 35:610-622.

Hogg, E.H., and P.Y. Bernier. 2005. Climate change impacts on drought-prone forestsin western Canada. For.Chron. 81:675-682

Hogg, E.H., and R.W. Wein. 2005. Impacts of drought on forest growth and regeneration following fire in southwestern Yukon, Canada. Can.J.For.Res. 35:2141-2150.

Johnson, E.A., and G.I. Fryer. 1989. Population dynamics in lodgepole pine-engelmann spruce forests. Ecology 70:1335-1345

Kenkel, N.C. 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. Ecology 69:1017-1024

Kenkel, N.C., M.L. Hendrie, and I.E. Bella. 1997. A long-term study of *Pinus banksiana* population dynamics. J.Veg.Sci. 8:241-254.

Larsen, C.P.S., and G.M. MacDonald. 1995. Relations between tree-ring widths, climate, and annual area burned in the boreal forest of Alberta. Can.J.For.Res. 25:1746-1755.

Liu, Y., and R.N. Muller. 1993. Effect of drought and frost on radial growth of overstorey and understorey stems in a deciduous forest. Am.Mid.Nat. 129:19-25.

Little, L.R. 2002. Investigating competitive interactions from spatial patterns of trees in multi-species boreal forests: the random mortality hypothesis revisited. Can.J.Bot. 80:93-100.

Mast, J.N., and T.T. Veblen. 1994. A dendrochronological method of studying tree mortality patterns. Phys.Geog. 15:529-542

McKenney, D.W., and J.H. Pedlar. 2003. Spatial models of site index based on climate and soil properties for two boreal tree species in Ontario, Canada. For.Ecol.Man. 175:497-507.

Nord-Larsen, T., C. Damgaard, and J. Weiner. 2006. Quantifying size-asymmetric growth among individual beech trees. Can.J.For.Res. 36:418-425

Oliver, C.D., and E.P. Stephens. 1978. Reconstruction of a mixed-species forest in Central New England. Ecology 58:562-572.

Orwig, D.A., and M.A. Abrams. 1997. Variation in radial growth responses to drought among species, site, and canopy strata. Trees Struct. Func. 11:474-484.

Piutti, E, and A. Cescatti. 1997. A quantitative analysis of the interactions between climatic response and intraspecific competition in European beech. Can.J.For.Res. 27:277-284

Schwinning, S., and J. Weiner. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia 113:447-455.

Stoll, P., J. Weiner, and B. Schmid. 1994. Growth variation in a naturally established population of *Pinus sylvestris*. Ecology 75:660-670.

Spittlehouse, D. 2005. Integrating climate change adaptation into forest management. For.Chron. 81:691-695

Swetnam, T.W., C.D. Allen, and J.L. Betancourt. 1999. Applied historical ecology: using the past to manage for the future. Ecol.Apps.9:1189-1206.

van den Brakel, J.A., and H. Visser. 1996. The influence of environmental conditions on tree-ring series of Norway spruce for different canopy and vitality classes. For.Sci. 42:206-219.

Volney, W.J.A. 1988. Analysis of historic jack pine budworm outbreaks in the Prairies provinces of Canada. Can.J.For.Res. 18:1152-1158

Volney, W.J.A. 1998. Ten-year mortality following a jack pine budworm outbreak in Saskatchewan. Can.J.For.Res. 28:1784-1793.

Volney, W.J.A., and K.I. Mallett. 1992. Light rings and the age of jack pine trees. Can.J.For.Res. 22:2011-2013

Vose, J.M., and W.T. Swank. 1994. Effects of long-term drought on the hydrology and growth of a white pine plantation in the southern Appalachians. For.Ecol.Man. 64:25-39.

Weiner, J. and O.T. Solbrig. 1984. The meaning and measurement of size hierarchies in plant populations. Oecologia 61:334-336.

Weiner, J., and S.C. Thomas. 1986. Size variability and competition in plant monocultures. Oikos 47:211-222.

Weiner, J. 1990. Asymmetric competition in plant populations. Trends.Ecol.Evol. 5:360-364.

Weiner, J. 1995. Follwing the growth of individuals in crowded plant populations. Trends.Ecol.Evol. 10:389-390.

Westoby, M. 1982. Frequency distributions of plant size during competitive growth of stands: the operation of distribution modifying functions. Ann.Bot. 50:733-735.

Wichmann, L. 2001. Annual variations in competition symmetry in even-aged sitka spruce. Ann.Bot. 88:145-151.

Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. Can.J.For.Res. 21:414-416

Zoladeski, C.A., G.M. Wickware, R.J. Delorme, R.A. Sims, and I.G.W. Corms. 1995. Forest ecosystem classification for Manitoba: field guide. Nat.Res.Can., Can.For.Serv., North.For.Cent., Edmonton, AB. Spec.Rep.2.

Table 1.1. Summary of select ecological, site, and stand characteristics of each study plot.

Region	Site	Ecological Type*	Soil Type*	Stump age** (year of origin)	DBH age** (year of origin)	Mean DBH (cm)	Mean Height (m)	Canopy Closure (%)	Live+ Dead Density (# ha^{-1})	Live Density (# ha^{-1})
Prince Albert (SK)	Rich	c1.3 jack pine-black spruce/feather moss	SD1 Dry/Sandy	78(1927)	73(1932)	14.2	14.6	70.6	3900	2200
	Poor	a1.1 jack pine/ bearberry/lichen	SV1 Very Dry/ Sandy	78(1927)	75(1930)	13.7	12.7	68.1	3300	2000
Candle Lake (SK)	Rich	c1.2 jack pine–black spruce/Labrador tea/feather moss	SM1 Moist/Sandy	88(1916)	82(1922)	17.4	15.9	84.9	1767	1267
	Poor	a1.1 jack pine/ bearberry/lichen	SV1 Very Dry/ Sandy	88(1916)	82(1922)	12.7	13.0	78.3	2556	1656
Flin Flon (SK)***	Rich	b4.1 white spruce (jack pine)/ blueberry-bearberry	SD1 Dry/Sandy	79(1926)	77(1928)	14.9	14.9	69.6	5300	1400
	Poor	a1.2 jack pine/ blueberry/lichen	SD1 Dry/Sandy	79(1926)	73(1932)	12.4	12.2	73.3	6300	1500
Jenpeg (MB)	Rich	v28 jack pine-black spruce/feather moss	S8 Moist Coarse Loamy	83(1922)	79(1926)	17.8	15.6	56.9	3000	1200
	Poor	v26 jack pine-black spruce/lichen	S3 Fresh Coarse Loamy	78(1927)	70(1935)	14.7	13.4	71.7	3700	1200
Thompson (MB)	Rich	v16 jack pine mixedwood/feather moss	S7 Moist Sandy	71(1933)	69(1935)	15.9	13.7	77.2	1900	1367
	Poor	v26 jack pine-black spruce/lichen	S1 Moderately Dry Sandy	71(1933)	67(1937)	9.4	8.0	59.5	3222	2089

* For the sites in Saskatchewan (SK), ecological and soil classificition is according to Beckingham et al (1996). For sites in Manitoba (MB), ecological and soil classification is according to Zoladeski et al (1995).

** Age refers to age of last sampled ring. The last sampled ring at Candle Lake and Thompson was 2004. At Prince Albert, Flin Flon, and Jenpeg, it was 2005.

*** The town of Flin Flon is located in the province of Manitoba, but the plots named Flin Flon are actually located in Saskatchewan.

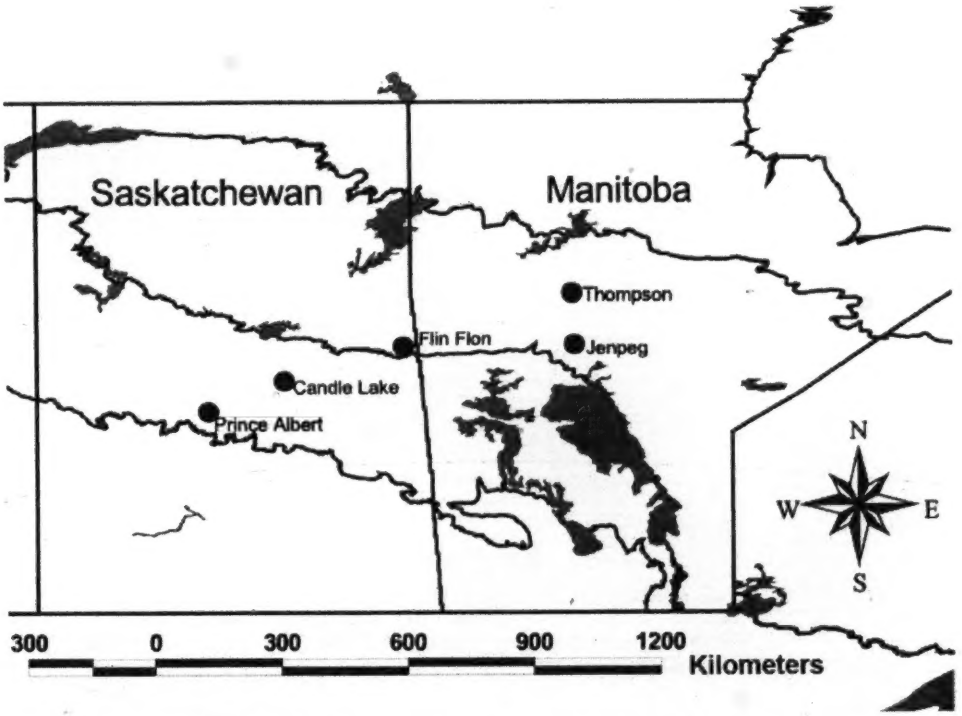

Figure 1.1. The location of the study plots. The Prince Albert and Candle Lake sites are located in the Boreal Plains ecozone. The Flin Flon, Thompson, and Jenpeg sites are located in the Boreal shield ecozone.

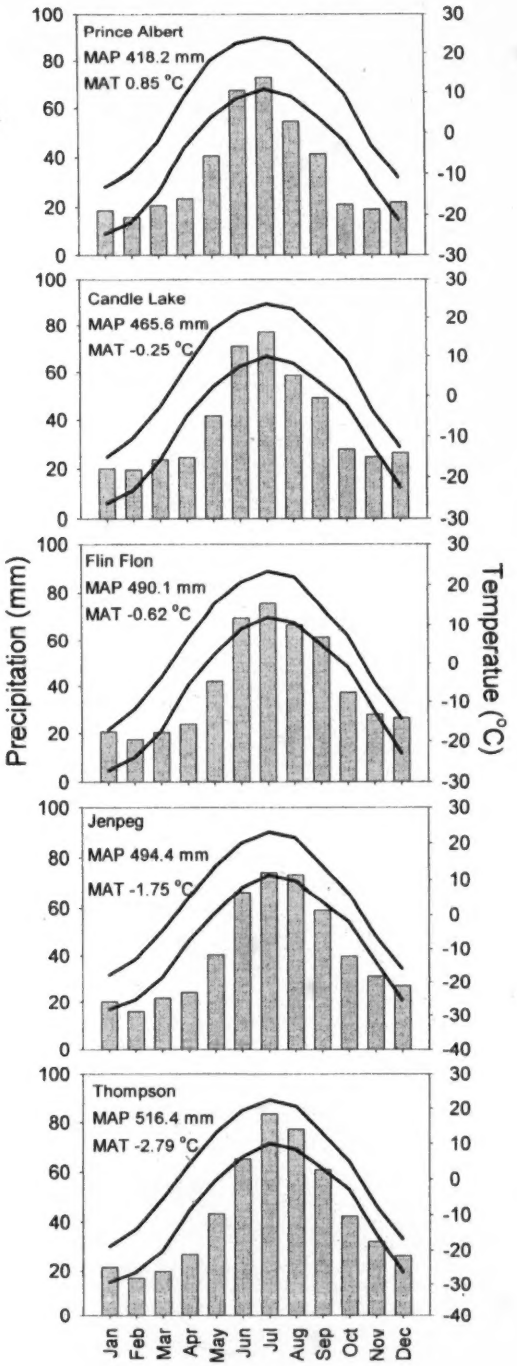

Figure 1.2. Climate normals at each study region based on data from 1970 to 2000. The bars represent mean precipitation by month. The upper dark line is the mean maximum monthly temperature, and the lower dark line is the mean minimum monthly temperature.

2.0 Accuracy of annual volume increment obtained by partial stem analysis, relative to full stem analysis

In this thesis, I use wood volume and volume increment to describe the size and growth rate of the study trees and stands. Presently, the best way of determining past annual volume increment of a tree is full stem analysis (e.g. Duff and Nolan 1953). However, full stem analysis is costly and destructive. Sample trees need to be felled and sectioned. Ring-widths need to be measured and cross-dated on each of these sections. Alternatively, annual diameter growth reconstructed from ring-widths measured only on a breast-height increment core could be used in combination with a height-diameter equation and a volume or taper equation to determine past volume increment. Using these reconstructed diameters with equations to estimate height and volume (hereinafter referred to as partial stem analysis) could be a less labour intensive and non-destructive way of determining past annual volume increment. Many studies have evaluated methods for measuring the standing volume of trees (e.g. Martin 1984, Biging 1988, Figueiredo-Filho and Schaaf 1999). Fewer have evaluated methods for measuring annual volume growth. This chapter assesses the accuracy of annual volume increment obtained using partial stem analysis by comparing increments obtained using this technique to those obtained from full stem analysis when both methods were applied to the same tree. This was done for three common boreal species: jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), and trembling aspen (*Poplus tremuloides*). The impact of different methods of determining volume was also assessed. Volume was estimated with either a region-specific parameterization of Kozak's (1988) taper equation or Honer et al's (1983) standard volume equation. Finally, the error in partial stem analysis techniques was discussed relative error presented in other mensurational studies.

2.1 Methods

2.1.1 Volume increment from full stem analysis

I obtained full stem analysis data for trees from two regions in the western Canadian boreal forest, one located near Prince Albert, Saskatchewan, and the other near Thompson, Manitoba. More details on the data can be found in Varem Sanders and Campbell (1998). Briefly, cross sections were taken at 1 m intervals, with additional samples at the stump, breast height, and base of the live crown. Two randomly oriented radii were measured on most samples using the DendroScan measurement system (Varem Sanders and Campbell 1996). At the time of sampling the jack pine (N=25) had an average diameter of 10.5 cm (range 4.1 to 18.8 cm) and an average height of 10.1 m (range 4.5 to 15.8 m). The trembling aspen (N=10) had an average diameter of 12.9 cm (range 5.7 to 17.2 cm) and an average height of 15.1 m (range 6.9 to 19.1 m). The black spruce (N=27) had an average diameter of 11.2 cm (range 4.0 to 17.6 cm) and an average height of 10.3 m (range 4.7 to 15.3 m). The TREEGLIA program (Bascietto and Scarascia-Mugnozza 2004) was used to calculate stem analysis volume increments from these data. More details on the algorithms used by TREEGLIA can be found in Bascietto and Scarascia-Mugnozza (2004). I used a series of custom data processing and

formatting programs written with Visual Basic for Applications for Microsoft Excel to convert data from DendroScan format to TREEGLIA input files. These were then input into TREEGLIA to calculate annual volume increment, expressed in $dm^3 year^{-1}$. For all subsequent comparisons, I took the full stem-analysis volume increments obtained with TREEGLIA to be the true (expected) value for this quantity.

2.1.2 Volume increment from partial stem analysis

I used the breast height sample taken from each tree was to obtain estimates of annual volume increment using partial stem analysis. Operationally, these samples would be obtained by extracting increment cores at breast height. The arithmetic average of the cumulative ring width in a given year from the two measured radii was taken as the measurement of diameter. To estimate volume increment from these diameters, three estimation equations were required. First, a bark thickness equation was used to estimate outside bark diameter, since diameters obtained from ring width measures are inside-bark diameters. Second, a height-diameter equation was used to estimate height increment from reconstructed outside-bark diameters. Third, a taper or volume equation was used to estimate volume from the diameter and height measurements.

Diameter inside bark (D_{ib}) was converted to diameter outside-bark (D_{ob}) and according to the following (Husch et al 2003)

$$D_{ib} = k\, D_{ob} \tag{2.1}$$

where D_{ib} is the inside bark diameter (cm), D_{ob} is the outside bark diameter (cm), and

k is a parameter to be estimated. Using bark-thickness data in Halliwell and Apps (1997), the estimates of this parameter were 0.964 (95% C.I. 0.961 to 0.966, n=221, r^2=0.99) for jack pine, 0.948 (95% C.I. 0.945 to 0.951, n=374, r^2=0.99) for black spruce and 0.945 (95% C.I. 0.941 to 0.949, n=186, r^2=0.99) for trembling aspen.

Heights were estimated from diameters using the Chapman-Richards function

$$H = 1.3 + a(1 - e^{-b \cdot D_{ob}})^c \tag{2.2}$$

where H is tree height (m), D_{ob} is outside bark diameter, and a, b, and c are parameters to be estimated. Data for fitting these equations were obtained from Halliwell and Apps (1997), supplemented with additional data collected as part of the present study. Equations were developed for each combination of species (jack pine, black spruce, and trembling aspen) and province (Saskatchewan, Manitoba). Non-linear regression with SYSTAT (Systat Software Inc, Point Richmond, CA) was used to estimate the parameters a, b, and c, using the Marquardt method. Several initial values were used for the fits to ensure that a global rather than local solution was achieved. The resulting parameter estimates and fit statistics are presented in Table 2.1.

Volumes were estimated from these height and diameter measurements using two possible equations. The first was the variable exponent taper equation of Kozak (1988)

$$D_{ib} = a_0 D_{ob}^{a1} a2^{D_{ob}} X_i^{b1 z_i^2 + b2 \ln(z_i + 0.001) + b3\sqrt{z_i} + b4 e^{z_i} + b5(D_{ob}/H)} \quad (2.3)$$

where D_{ib} is inside bark diameter at height i along the stem (cm), D_{ob} is the diameter at breast height (cm), H is the total height (m) of the tree outside bark, and other components of the equation are as defined in Kozak (1988). Parameters *a0*, *a1*, *a2*, *b1*, *b2*, *b3*, *b4*, and *b5* for sites in Saskatchewan were obtained from Gal and Bella (1994), and for sites in Manitoba from Klos (2004), and are presented in Table 2.2. Total volumes were determined using numerical integration algorithms presented in Klos (2004). The second was Honer et al's (1983) standard volume equation:

$$V = a_1 D_{ob}^{\ 2} (1 - a_2 b_2)^2 / (c_1 + (a_3 c_2 / H)) \quad (2.4)$$

where V is the total volume, a_1, a_2, and a_3 are metric conversion factors, D_{ob} is diameter at breast height, H is total height, and b_2, c_1, and c_2 are species-specific parameters. Conversion factors and parameters for each species were obtained from Honer et al, (1983), and are presented in Table 2.3. For both equations, volume increment for each tree was obtained by subtracting the volume in year y-1 from the volume in year y, and was expressed in $dm^3 year^{-1}$.

2.1.3 Accuracy assessment

Two methods of determining volume increment were compared: [1] heights predicted using a height-diameter equation (Eq. 2) and Kozak's (1988) taper equation (Eq. 3), and [2] heights predicted using a height-diameter equation (Eq. 2) and Honer et al's (1983) standard volume equation (Eq. 4). Only measurements when trees had a dbh > 4 cm were used, resulting in a total of n=830 observed-estimated volume increment pairs that could be compared for jack pine, n=1612 for black spruce, and n=385 for trembling aspen. Errors were assessed using the DOSATEST program (Wiant 1993) that implements the accuracy test described in Reynolds (1984). The relative mean error and its 95% confidence intervals was used to assess the accuracy of volume increments determined by each of the methods, relative to the volume increments obtained from full stem analysis and considered unbiased when the 95% confidence interval contained zero. These are the same methods as used by Newton (2004) to assess the impact of different sampling strategies on stem analysis volume estimation.

2.2 Results

The mean absolute and relative errors and 95% confidence intervals for each of the two methods compared are presented in Table 2.4. Based on the 95% confidence intervals, both volume estimation methods were biased for jack pine. For trembling aspen and black spruce, volume estimated with Honer et al's (1983) was biased, while volume estimated with Kozak's (1988) taper equation was not. Within a species, the

95% confidence intervals indicated that they were not significantly different. Overall, method (1), which used Kozak's (1988) taper equation and heights predicted from a height-diameter equation provided the best combination of accuracy and ease of data collection. The magnitude of the relative prediction error for method (1) was 7.24% (95% CI 4.83 to 9.65) for jack pine, 0.79% (95% CI -2.55 to 4.13) for trembling aspen, and 2.29% (95% CI -0.86 to 3.72).

2.3 Discussion

For each species, the absolute value of the relative error for method (1), which had the best combination of accuracy and ease of data collection, was less than 10%. Some error is inevitable in mensurational studies, so a comparison of measurement methods requires a definition of how much is tolerable (Freese 1960). Errors as large as 10% are commonly reported in many mensurational studies. For example, stem eccentricity results in errors depending upon the shape of the tree and the type of instrument used to measure diameter. Gregoire et al (1990) found an average difference of 5% in basal area based depending on whether diameter was measured with a tape or calipers. Biging and Wensel (1988) found basal area error to range from -4.87% to 7.37% depending on what assumptions were made about the cross-sectional shape of the stem. Errors can also occur depending on the standard log formula (i.e. Newton's, Smalian's, or Huber's (Husch et al 2003)) used to determine volume. Martin (1984) found total volume estimation bias to range from 0.86 to 3.51% for ten different volume estimation equations in eastern hardwoods. Biging (1988) found volume estimation error to range from 2 to 9% for white fir (*Abies concolor*), depending upon the estimation method. Figueiredo-Filho and Schaaf (1999) found that the best method for estimating the volume of slash pine (*Pinus elliotii*) from a single dbh measurement had an error of 9.7% when compared to true volumes measured with a xylometer. Annual field measurements of diameters and heights could also be used to estimate volume increments in this way. However, error induced by not measuring exactly at breast height or at precisely the same location each time and by the difficulty of measuring height in dense forests reduces the accuracy of field measurements. Overall, volume increment estimates from partial stem analysis are in the range of error of other mensurational studies.

Few other studies have compared the relative accuracy of different methods of measuring the annual incremental growth of trees. LeBlanc (1990) and Bouriad et al (2005) found that growth series at breast height were highly correlated with whole-tree volume or biomass increment series in high-elevation red spruce (*Picea rubens*) and European beech (*Fagus sylvatica*), but did not estimate the level of error. Newton (2004) compared the accuracy of different full stem analysis sampling protocols for measuring volume increment in jack pine, and found that mean prediction error was reduced and precision was increased by increasing the number of heights at which radii were measured from 5 to 10, and by measuring more radii at each height. However, this would require 5 to 10 times more sampling effort than the partial stem analysis method in the present study, and would preclude further measurement of the growth of sample trees because it requires destructive sampling. The importance of the improved estimates

obtained of the full stem analysis protocols described by Newton (2004) would need to be determined by study objectives.

Most studies of tree growth do not measure volume or volume increment directly. Instead, they measure either diameter and/or height, and use a series of equations to predict volume based on these measurements. The best available equations for scaling growth at breast height to whole tree growth are constantly being improved. In this chapter, the methods were selected because I could estimate parameters from readily available data, or because I could obtain parameters for them from the existing literature for my study region. They could easily be replaced by other equations, particularly those that are sensitive to the effect of stand conditions and competitive effects on height-diameter relationships (e.g. Sharma and Zhang 2004) or tree taper (e.g. Morris and Forslund 1992, Muhairwe et al 1994), which should consequently improve the estimates of annual volume increment that could be obtained. These improvements would be relatively small since the mean prediction errors from the best techniques in this study were already less than 10%. Even with relatively simple equations for estimating height and volume, partial stem analysis techniques provided acceptably accurate measurements of annual volume increment of individual trees. Annual volume increment data are important for assessing the effects of transient factors like insect defoliation or drought on tree growth and stand development (e.g. Wichmann 2001, Hogg et al 2005, Hogg and Wein 2005). The results of this chapter show that partial stem analysis should yield results equal to full stem analysis in such studies because it provides acceptable estimates of volume increment.

2.5 Literature Cited

Bascietto, M., and G. Scarascia-Mugnozza. 2004. A collection of functions to determine annual tree carbon increment via stem analysis. Ann.For.Sci. 61:597-602.

Biging, G.S., and L.C. Wensel. 1988. The effect of eccentricity on the estimation of basal area and basal area increment of coniferous trees. For.Sci. 34:621-633.

Biging, G.S. 1988. Estimating the accuracy of volume equations using taper equations of stem profile. Can.J.For.Res. 18:1002-1007.

Bouriaud, O., N. Breda, J-L. Dupouey, and A.Granier. 2005. Is ring width a reliable proxy for stem-biomass increment? A case study in European beech. Can.J.For.Res. 35:2920-2933.

Duff, G.H., and N.J. Nolan. 1953. Growth and morphogenesis in the Canadian forest species. I. The controls of cambial and apical activity in *Pinus resinosa.* Can.J.Bot. 31:471–513.

Freese, F. 1960. Testing accuracy. For.Sci. 6:345-354.

Filliben, J.J. 1975. The probability plot correlation coefficient test for normality. Technometrics 17:111–117.

Figueiredo-Filho, A., and L.B. Schaaf. 1999. Comparison between predicted volumes estimated by taper equations and true volumes obtained by the water displacement technique (xylometer). Can.J.For.Res. 29:451-461.

Gál, J., and I.E. Bella. 1994. New stem taper functions for 12 Saskatchewan timber species. Nat.Res.Can., Can.For.Serv., North.For.Cent., Edmonton, AB. Inf. Rep. NOR-X-338.

Gregoire, T.G., S.M. Zedaker, and N.S. Nicholas. 1990. Modeling relative error in stem basal area estimates. Can.J.For.Res. 20:496-502.

Halliwell, D.H., and M.J. Apps. 1997. Boreal Ecosystem-Atmosphere Study (BOREAS) biometry and auxiliary sites: overstory and understory data. Nat.Res.Can., Can.For.Serv., North.For.Cent., Edmonton, AB.

Hogg, E.H., J.P. Brandt, and B. Kochtubajda. 2005. Factors affecting interannual variation in growth of western Canadian aspen forests during 1951-2000. Can.J.For.Res. 35:610-622.

Hogg, E.H., and R.W. Wein. 2005. Impacts of drought on forest growth and regeneration following fire in southwestern Yukon, Canada. Can.J.For.Res. 35:2141-2150.

Honer, T.G., M.F. Ker, and I.S. Alemdag. 1983. Metric timber tables for the commercial tree species of central and eastern Canada. Env.Can., Can.For.Serv., Mar.For.Res.Cent., Fredericton, NB. Inf. Rep. M-X-140.

Husch, B, T.W. Beers, and J.A. Kershaw. 2003. Forest Mensuration, 4th Ed. John Wiley and Sons, Hoboken, NJ.

Klos, R. 2004. Ecologically based taper equations for major tree species in Manitoba. Dissertation, Lakehead University, Thunder Bay, Canada.

Kozak, A. 1988. A variable-exponent taper equation. Can.J.For.Res. 18:1362-1368.

LeBlanc, D.C. 1990. Relationship between breast-height and whole-stem growth indices for red spruce on Whiteface Mountain, New York. Can.J.For.Res. 20:1399-1407.

Martin, A.J. 1984. Testing volume equation accuracy with water displacement techniques. For.Sci. 30:41-50.

Morris, D.M., and R.R. Forslund. 1992. The relative importance of competition, microsite, and climate in controlling the stem taper and profile shape in jack pine. Can.J.For.Res. 22:1999-2003.

Muirhawe, C.K., V.M. LeMay, and A. Kozak. 1994. Effects of adding tree, stand, and site variables to Kozak's variable-exponent taper equation. Can.J.For.Res. 24:252-259.

Newton, P.F. 2004. A stem analysis computational algorithm for estimating volume growth and its empirical evaluation under various sampling strategies. Comp.Elect.Ag. 44:21-31.

Reynolds, M.R. 1984. Estimating the error in model predictions. For.Sci. 30:454-469.

Sharma, M., and S.Y. Zhang. 2004. Height-diameter models using stand characteristics for Pinus banksiana and Picea mariana. Scand.J.For.Res. 19:442-451.

Varem-Sanders, T.M.L., and I.D. Campbell. 1996. DendroScan: A Tree-Ring Width and Density Measurement System. UBC Press, Vancouver 132p.

Varem-Sanders, T.M.L., and I.D. Campbell. 1998. Boreal Ecosystem-Atmosphere study (BOREAS) biometry and auxiliary sites: X-ray densitometry of tree allometry samples. Nat.Res.Can., Can.For.Serv., North For.Cent., Edmonton, AB.

Wiant, H.V. 1993. DOSATEST for testing accuracy. Compiler 11:28-29.

Wichmann, L. 2001. Annual variations in competition symmetry in even-aged sitka spruce. Ann.Bot. 88:145-151.

Table 2.1. Parameter estimates and fit statistics for the height-diameter equation

Species	N	A	b	c	r^2
Saskatchewan					
Jack Pine	392	18.866	0.105	1.482	0.98
		(17.541 20.191)	(0.079, 0.131)	(1.143 1.820)	
Black Spruce	143	13.752	0.215	3.432	0.97
		(12.199 15.305)	(0.140, 0.291)	(1.711, 5.154)	
Trembling Aspen	145	24.420	0.084	1.482	0.98
		(21.419 27.420)	(0.051, 0.118)	(1.005 1.956)	
Manitoba					
Jack Pine	394	19.648	0.081	1.563	0.98
		(17.408 21.888)	(0.061, 0.101)	(1.290 1.837)	
Black Spruce	215	13.391	0.145	1.883	0.97
		(11.247 15.535)	(0.089, 0.202)	(1.281 2.486)	
Trembling Aspen	84	21.268	0.113	1.824	0.97
		(18.518 24.018)	(0.067, 0.159)	(1.122 2.526)	

Table 2.2. Parameters for Kozak's (1988) taper equation

Parameter	Jack Pine	Aspen	Black Spruce
Saskatchewan*			
a0	0.7382	0.7589	0.9333
a1	1.0803	1.0530	0.9930
a2	0.9950	0.9965	0.9980
b1	0.9465	-0.1487	1.6340
b2	-0.2153	0.0679	-0.3773
b3	1.5298	-1.8923	2.8393
b4	-0.7693	1.0091	-1.5238
b5	-0.1670	0.0764	0.2250
Manitoba*			
a0	0.9690	0.6549	0.8894
a1	0.9568	1.1280	1.0163
a2	1.0012	0.9930	0.995
b1	-0.0805	0.9923	0.2866
b2	-0.0659	-0.1311	-0.0853
b3	0.4314	0.6458	0.6307
b4	0.1196	-0.2967	-0.1714
b5	-0.0685	0.0670	0.1491

* Saskatchewan parameters were obtained from Gal and Bella (1994), and Manitoba parameters from Klos (2004).

Table 2.3. Parameters (b2, c1 and c2) and metric conversion factors (a1, a2, and a3) for Honer et al's (1983) standard volume equation

Parameter	Jack Pine	Aspen	Black Spruce
a1	0.0043891	0.0043891	0.0043891
a2	0.04365	0.04365	0.04365
a3	0.3048	0.3048	0.3048
b2	0.151	0.127	0.164
c1	0.891	-0.312	1.588
c2	348.53	436.683	333.364

Table 2.4. Absolute and relative prediction errors of using partial stem analysis techniques to estimate the annual volume increment of jack pine, aspen and black spruce, relative to full stem analysis. Error values in bold were considered the correct estimates of the error for that method.

Species	Volume Equation	Error Type (units)	Mean Error (D) (n)	Normality of Errors (r)	10% Trimmed Mean Error (D_t) (n)	95% Confidence Interval for (D_t)
Jack Pine	(1) Kozak	Absolute (dm^3)	0.18 (830)	0.9479*	**0.12 (664)**	$0.08 \leq D_t \leq 0.16$
		Relative (%)	11.23 (830)	0.9625*	**7.24 (664)**	$4.83 \leq D_t \leq 9.65$
	(2) Honer	Absolute (dm^3)	-0.11 (830)	0.9735*	**-0.12 (664)**	$-0.15 \leq D_t \leq -0.09$
		Relative (%)	-6.74 (830)	0.9561*	**-9.78 (664)**	$-11.62 \leq D_t \leq -7.94$
Aspen	(1) Kozak	Absolute (dm^3)	-0.04 (385)	0.9524*	**-0.05 (308)**	$-0.11 \leq D_t \leq 0.01$
		Relative (%)	4.75 (385)	0.9305*	**0.79 (308)**	$-2.55 \leq D_t \leq 4.13$
	(2) Honer	Absolute (dm^3)	-0.28 (385)	0.9634*	**-0.25 (308)**	$-0.31 \leq D_t \leq -0.19$
		Relative (%)	-7.16 (385)	0.9309*	**-10.67 (308)**	$-13.62 \leq D_t \leq -7.72$
Black Spruce	(1) Kozak	Absolute (dm^3)	0.06 (1612)	0.9675*	**-0.001 (1290)**	$-0.012 \leq D_t \leq 0.011$
		Relative (%)	**2.29 (1612)**	0.9881		$-0.86 \leq D \leq 3.72$
	(2) Honer	Absolute (dm^3)	-0.06 (1612)	0.9634*	**-0.06 (1290)**	$-0.07 \leq D_t \leq -0.05$
		Relative (%)	**-7.96 (1612)**	0.9931		$-9.12 \leq D \leq -6.78$

* Errors are not normally distributed at the 0.05 level according to the normal probability plot correlation test (Filliben 1975). As a result, the 10% trimmed means and jackknife variance estimates were used to calculate approximate 95% confidence intervals

3.0 Dendrochronological reconstruction of snag and downed log dynamics[1]

Coarse woody debris influences numerous ecological functions, including nutrient cycling (e.g. Laiho and Prescott 2004), forest carbon dynamics (e.g. Howard et al 2004, Nalder and Wein 2006, Shaw et al 2006), and forest fire behaviour (e.g Nalder et al 1999). Understanding spatial and temporal mortality patterns are also central to investigating forest stand dynamics (Johnson and Fryer 1989, Oliver and Larson 1996). Many boreal stands are established after fire, tend to be even-aged and consist of few tree species. In such forests, accumulation of coarse woody debris has been observed to follow a "U-shaped" successional pattern, with high abundance immediately following fire disturbance, low abundance during mid-successional stages, and increasing abundance again during late-successional stages (Brais et al 2005, Brassard and Chen 2006).

This chapter examines the dynamics of snags and downed logs at my study plots. Past studies of the stand dynamics of jack pine observed that snags and downed logs of this species appear to be persistent but did not quantitatively assess the period of their persistence (Yarranton and Yarranton 1975, Kenkel 1988). Annual data on the growth and dynamics of forest stands can often be obtained by measuring ring widths and cross-dating the year of death of standing snags and downed logs (e.g. Henry and Swan 1974, Oliver and Stephens 1976, Stoll et al 1994, Carrer and Urbinati 2001). The period of persistence of snags and downed logs can be used to assess how far back in time growth and stand dynamics can be reconstructed with these techniques (Johnson and Fryer 1989, Mast and Veblen 1994). The goals of this chapter are to determine how long jack pine snags and downed logs persist by cross-dating their year of death and to use these data on age at death to estimate mortality trajectories, the fall rate of snags and the time since falling of downed logs. Also, because all attempts at historical reconstruction in ecology suffer from the problem of decreasing reliability with increasing time from the present, the results of the study are also discussed in relation to the question of how far into the past dendrochronological methods can reliably reconstruct the growth and dynamics of jack pine forests in this region.

3.1 Methods

3.1.1 Field and laboratory

Field data collection and laboratory sample processing was conducted as described in chapter 1.

3.1.2 Estimating year of death for decomposed samples

Ring widths could be measured to the bark along 2 radii on dateable samples. More snags (95.5% of n = 308) than downed logs (64.8% of n=291) could be dated.

---

[1] A version of this chapter has been published. Metsaranta, J.M., Lieffers, V.J., and Wein, R.W. 2007. Dendrochronological reconstruction of jack pine snag and downed log dynamics in Saskatchewan and Manitoba, Canada. Forest Ecology and Management. doi:10.1016/j.foreco.2007.10.030

Absence of ring-widths for decomposed trees results in missing data for year of death. The diameter of a decomposed tree was used to estimate its ring-widths and year of death. The mean year of death of the 3 larger and 3 smaller trees nearest in diameter, of the same class (snag or downed log), and at the same plot as a decomposed tree, was used as an estimate of its year of death. To test the accuracy of this method, age of death was calculated in the same way for 84 randomly selected trees (6 from each 100 m^2 plot 12 from each 900 m^2 plot) where the age of death was known by cross dating.

3.1.3 Plot mortality trajectories

Cumulative mortality in jack pine follows a sigmoidal pattern (Yarranton and Yarranton 1975, Kenkel et al 1997), so I fit a Richards function (Sit and Poulin-Costello 1994) to the cumulative proportional mortality data from each site

$$M = a\left(1 - e^{-b \cdot A}\right)^{c} \tag{3.1}$$

where M is cumulative mortality, A is stand age. Parameters *a, b,* and *c* were estimated using non-linear regression with SYSTAT (Systat Software Inc, Point Richmond, CA). The estimated parameters were then used to examine the mortality rate using the derivative of the Richards function (Eq.3.2) and the acceleration in mortality rate using the second derivative of the Richards function (Eq.3.3).

$$\frac{dM}{dA} = abce^{-bA}\left(1 - e^{-bA}\right)^{-1+c} \tag{3.2}$$

$$\frac{d^2M}{dA^2} = a\left(b^2(-1+c)ce^{-2bA}\left(1 - e^{-bA}\right)^{-2+c} - b^2ce^{-bA}\left(1 - e^{-bA}\right)^{-1+c}\right) \tag{3.3}$$

3.1.4 Fall rate and time since falling

Snag fall rate was estimated by the method of Gore et al (1985). It assumes that fall rate *S* follows a negative exponential curve

$$S(t) = e^{(-\theta t)}, \quad t \geq 0 \tag{3.4}$$

where *t* is time and $1/\theta$ is the average length of time that a tree stands. When a tree falls is not directly observed in a dendrochronological study. What is observed is the time since death, and if it is currently a snag or a downed log. A snag has stood at least as long as its time since death so it is "right" censored. A downed log stood at most as long as its time since death so it is "left" censored. Gore et al (1985) provide an equation that can be solved iteratively to obtain the maximum likelihood estimate of θ from such data

$$\sum_{i=1}^{m} X_i = \sum_{j=m+1}^{n} \left(\frac{X_j}{e^{(\theta X_j)} - 1} \right) \tag{3.5}$$

where n is the total number of dead trees dated, $i=1$ *to* m are the time since death values for m trees (X_i) that are snags at the time of sampling, and $j = m+1$ *to* n are the time since death values for n-m trees (X_j) that are downed logs at the time of sampling. Gore et al (1985) also gave an equation for expected snag standing time conditional on the fact that the time it has stood (X_s) has to be less than or equal to its time since death (X)

$$E(X_s | X_s \leq X) = \frac{1 - e^{(-\theta X)} - \theta X e^{(-\theta X)}}{\theta \left(1 - e^{(-\theta X)}\right)} \tag{3.6}$$

The time that a downed log has been in the ground is determined by subtracting the result of equation 3 from its time since death. Though this assumes a constant snag input rate (which may not always be reasonable (Johnson and Greene 1991)), its results do not differ significantly from methods not making this assumption when both are applied to the same data (Storaunet and Rolstad 2004).

These methods provide fall rates in units of trees year^{-1}, without an area basis because the calculated fall rate is meant to apply to the individual tree. For example, if the fall rate is 0.01 trees year^{-1}, then on an area of 1 ha with 1000 dead trees, about 10 trees will fall in a year. For a single dead tree, the expected standing time will be 100 years. In order to apply this rate in, for example, an individual tree growth model, data on the number of dead trees in the plot being modeled would need to be known, but the model could use a plot of any size.

3.2 Results

3.2.1 Snag and downed log persistence

Figure 3.1 plots snag and downed log age at death, time since death and year of death. The earliest dateable snag died 70 years before sampling (in 1935), at age 18. The earliest dateable downed log died 62 years before sampling (in 1943), at age 21. Nine trees dying more than 55 years before sampling (before 1950) were found. Downed log year of death peaked 23 to 45 years before sampling (between 1960 and 1982). Four downed logs dying less than 15 years before sampling (since 1990) were found. Snag year of death peaked 18 to 26 years before sampling (between 1979 and 1987). Trees began to die around age 20, with significant numbers dying after age 30, or 55 years before sampling (in 1950).

3.2.2 Accuracy of year of death estimates

Measured year of death and its estimate from the 6 trees at a plot nearest in size and of the same class was significantly correlated (r^2=0.88, $p<0.001$, Figure 3.2) for 84 random trees. The slope of the regression line between the two measures was not

significantly different from 1 (Slope = 0.93, 95% CI 0.86 to 1.01, Figure 3.2). The mean absolute difference between them was 3.3 (SD 2.4) years.

3.2.3 Plot mortality trajectories

Figure 3.3 plots the proportional cumulative mortality for each plot, fit to the Richards function. Figure 3.4 plots the resulting estimates of the mortality rate and mortality rate acceleration. Table 3.1 presents information on the inflection points in mortality rate and acceleration and, for comparison, the same information for jack pine mortality data from Kenkel et al (1997), also fit to the Richards function. The maximum mortality rate ranged from 0.87% for the poor site at Prince Albert to 3.25% for the poor site at Flin Flon. The age which the mortality rate peaked was identical or very similar in each region, and ranged from 38 years for the rich site at Thompson to 66 years for the rich site at Prince Albert. The age of maximally accelerating mortality also occurs at very similar times in each region, and ranges from 25 years for the rich site at Thompson to 42 years for the rich site at Candle Lake. The maximal acceleration in mortality ranged from 0.030 % $year^{-2}$ for the rich site at Prince Albert to 0.315 % $year^{-2}$ for the poor site at Flin Flon. Overall, the sites in this study have lower maximum mortality and mortality acceleration rates than Kenkel et al (1997), and these inflection points occur later than they do in Kenkel et al (1997).

3.2.4 Fall rate and time since falling

Table 3.2 presents snag fall rates and mean, median, and 80th percentile of snag standing times for each site. Average fall rate was 0.026 trees $year^{-1}$(SD 0.012) at rich sites, 0.030 trees $year^{-1}$(SD 0.015) at poor sites, and ranged from 0.014 trees $year^{-1}$ for the poor site at Prince Albert to 0.050 trees $year^{-1}$ for the poor site at Jenpeg. Figure 3.5 plots time since falling and year of fall of downed logs. The oldest fell 43 years prior to sampling (in 1963), and most fell 10 and 30 year prior to sampling (from 1975 and 1995).

3.3 Discussion

The oldest jack pine snag in this study died 70 years prior to sampling (in 1935), and the oldest dateable downed log died 62 years prior to sampling (in 1943). Other studies have also shown that snags and downed logs can be very persistent. In subalpine forests in Colorado, Brown et al (1998) found downed *Pinus contorta* logs persisting up to 139 years. Mast and Veblen (1994) found *Picea engelmanii* snags persisting up to 184 years. In their study of jack pine, Yarranton and Yarranton (1975) were able to identify and date 0.75 dead trees m^{-2} (7500 dead trees ha^{-1}) at a 56 year old stand, indicating that a persistence time of 50 years or more for dead jack pine trees is reasonable. Snag fall rate for jack pine ranged from 0.014 to 0.050 trees $year^{-1}$. This is comparable to rates for *Pinus contorta* and *Picea engelmanii* snags (0.020 to 0.064 trees $year^{-1}$) in Johnson and Greene (1991), and rates for *Picea abies* (0.033 trees $year^{-1}$ when using the same method as the present study) in Storaunet and Rolstad (2004).

The technique of estimating the year of death for decomposed trees from the mean year of death of the 6 snags or logs nearest in diameter was unbiased with a mean absolute difference of 3.3 years between the true and estimated year of death. Other studies have shown that decay class may not (Mast and Veblen 1994, Daniels et al 1997)

be a reliable indicator of time since death, and that using additional variables like the number of branch orders (e.g. Storaunet 2004) or the presence of bark (e.g. Newberry et al 2004) can improve predictions of time since death. The method of estimating the year of death from the year of death of similar trees that was used in this paper had a higher correlation (R^2=0.88) between the observed and predicted years of death than the models in Storaunet (2004) (R^2 = 0.67 to 0.71), and most models in Newberry et al (2004) (R^2 = 0.78 to 0.95). This suggests that the method used here is comparable to others presently used to estimate the year of death of snags and logs when it cannot be determined either by observation or by cross-dating.

Like all historical reconstruction methods in ecology (Swetnam et al 1999), the reliability of dendrochronological stand reconstruction techniques decreases with increasing time from the present. In the case of this study, this decline in reliability occurred because many small trees that died early in the life of these stands likely decomposed to the extent that they could not be detected at the time they were sampled for this study. Estimating the length of this reliable reconstruction period was one of the goals of this paper. In previous studies, Johnson and Fryer (1989) showed that the reliable dendrochronological reconstruction period for subalpine lodgepole pine-engelmann spruce forests was the second half of a stand's history, regardless of its age. The stands in this study ranged in age from 79 to 90 years, suggesting a reliable reconstruction age of 40 to 50 years into the past. The other lines of evidence from the results of the present study also support the contention that 50 years is a reasonable estimate of the reliable period for dendrochronological reconstruction of jack pine forests in this region. First, the observed timing of mortality at the study plots, i.e., relatively late in stand development, is likely a true estimate of mortality, it matches the timing that would be expected from self-thinning. Using permanent sample plots, Kenkel et al (1997) showed that rapid self-thinning in their study occurred 25-46 years after establishment. The estimates of maximum mortality rate (4.42%) , the age at which mortality rate peaked (30 years), maximum change in mortality rate (0.525 % $year^{-2}$), and the age at which mortality changed fastest (23 years) were all higher and occurred earlier than estimates from the present study. Kenkel et al (1997) assumed that self thinning began at age 25, which was close to the year that the mortality rate changed maximally. In this study, the average age at which mortality rate changed maximally was 34, and if all sites are taken together, was close to the time that larger numbers of trees begin dying. This occurred in 1955, at age 30, or about 50 years prior to sampling. The average origin of stands in this study was 1925, indicating that dead trees began to appear at the time at which self-thinning would be expected to occur.

The second line of evidence for the ability to reliably reconstruct jack pine stands 50 years into the past comes from observations of the slow decomposition rate of downed logs. Alban and Pastor (1993) noted that jack pine wood had the lowest decomposition rate of four species tested, and calculated a half-life of 16 years. A study by Trofymow et al (2002) examined the decomposition rate of various types of litter across Canada, though it used western hemlock (*Tsuga heterophylla*) and not jack pine wood. Based on parameters from the sites from Trofymow et al (2002) that are nearest to those in the present study, the half-life of wood would be 30 years at Jenpeg and Thompson and 77 years at Prince Albert, Candle Lake, and Flin Flon. Trofymow et al (2002) found

decomposition to vary as a function of temperature and precipitation. A site that is slightly to the north and colder than Thompson had a wood half-life of 346 years, one slightly to the south and warmer than Prince Albert had a wood half-life of 15 years. The average wood half-life in Trofymow et al (2002) was 48 years (SD 85.3 years). The oldest downed log was estimated to have fallen 43 years ago, and most to have fallen 10 to 30 years ago, and so fell to the ground within the time that they would be expected to persist, on average, based on decomposition rates observed by Trofymow et al (2002).

3.4 Conclusion

Snags and downed logs influence many ecological functions, so long-term annual data on their dynamics is necessary for developing or validating many ecological models. The results of this study show that data obtained by the combination of dendrochronology and stand reconstruction techniques used in this study can reliably obtain annual data on the dynamics of snags and downed logs up to 50 years into the past in maturing jack pine forests in this region. The dynamics of snags and downed logs are presently monitored by periodically measuring permanent sample plots. While permanent plots offer more precise measurements at each measurement time, the stand reconstruction techniques used in this study have several advantages over reliance on permanent sample plots: the data are at an annual resolution, they follow the growth and mortality of individuals over time, and data can be obtained relatively quickly in areas, such as this study area, where there are few long-term permanent plots.

3.5 Literature Cited

Alban, D.H., and J. Pastor. 1993. Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. Can.J.For.Res. 23:1744-1749

Brais, S., F. Sadi, Y. Bergeron, and Y. Grenier. 2005. Coarse woody debris dynamics in a post-fire jack pine chronosequence and its relation with site productivity. For.Ecol.Man. 220:216-226

Brassard, B.W., and H.Y.H. Chen. 2006. Stand structural dynamics of North American boreal forests. Crit.Rev.Plant.Sci. 25:115-137

Brown, P.M., W.D. Sheppard, S.A. Mata, and D.L. McClain. 1998. Longevity of windthrown logs in a subalpine forest of central Colorado. Can.J.For.Res. 28:932-936

Carrer, M., and C. Urbinati. 2001. Spatial analysis of structural and tree-ring related parameters in a timberline forest in the Italian Alps. J.Veg.Sci. 12:643-52

Daniels, L.D., J. Dobry, K. Klinka, and M.C. Feller. 1997. Determining year of death of logs and snags of *Thuja plicata* in southwestern coastal British Columbia. Can.J.For.Res. 27:1132-1141

Gore, A.P., E.A Johnson, and H.P. Lo. 1985. Estimating the time a dead tree has been on the ground. Ecology 66:1981-1983

Howard, E.A., S.T. Gower, J.A. Foley, and C.J. Kucharik. 2004. Effects of logging on carbon dynamics of a jack pine forest in Saskatchewan, Canada. Glob.Change Biol. 10:1267-1284

Henry, J.D., and J.M.A. Swan. 1974. Reconstructing forest history from live and dead plant material – an approach to the study of forest succession in southwest New Hampshire. Ecology 55:772-783

Johnson, E.A., and G.I. Fryer. 1989. Population dynamics in lodgepole pine-engelmann spruce forests. Ecology 70:1335-1345

Johnson, E.A., and D.F. Greene. 1991. A method for studying dead bole dynamics in *Pinus contorta* var. *latifolia* - *Picea engelmanii* forests. J.Veg.Sci. 2:523-530

Kenkel, N.C. 1988. Patterns of self-thinning in jack pine: testing the random mortality hypothesis. Ecology 69:1017-1024

Kenkel, N.C., M.L. Hendrie, and I.E. Bella. 1997. A long-term study of *Pinus banksiana* population dynamics. J.Veg.Sci. 8:241-254

Laiho, R., and C.E. Prescott. 2004. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. Can.J.For.Res. 34:763-777

Mast, J.N., and T.T. Veblen. 1994. A dendrochronological method of studying tree mortality patterns. Phys.Geog. 15:529-542

Nalder, I.A., R.W. Wein, M.E. Alexander, and W.J. de Groot. 1999. Physical properties of dead and downed round-wood fuels in the boreal forests of western and northern Canada. Int.J.Wild.Fire. 9:85-99

Nalder, I.A., and R.W. Wein. 2006. A model for the investigation of long-term carbon dynamics in boreal forests of western Canada I. Model development and validation. Ecol.Mod. 192:37-66

Newbery, J.E., K.J. Lewis, and M.B. Walters. 2004. Estimating time since death of *Picea glauca* × *P. engelmannii* and *Abies lasiocarpa* in wet cool sub-boreal spruce forest in east-central British Columbia. Can.J.For.Res. 34:931-938

Oliver, C.D., and E.P. Stephens. 1978. Reconstruction of a mixed-species forest in Central New England. Ecology 58:562-572

Oliver, C.D., and B.C. Larson. 1996. Forest Stand Dynamics. John Wiley and Sons, NY.

Shaw, C., O. Chertov, A. Komarov, J. Bhatti, M. Nadporozskaya, M. Apps, S. Bykhovets, and A. Mikhailov. 2006. Application of the forest ecosystem model EFIMOD 2 to jack pine along the Boreal Forest Transect Case Study. Can.J.Soil Sci. 86:171-185

Sit, V., and M. Poulin-Costello. 1994. Catalog of curves for curve-fitting. Biometrics Information Handbook Series No. 4. British Columbia Ministry of Forests, Victoria, B.C.

Stoll, P., J. Weiner, and B. Schmid. 1994. Growth variation in a naturally established population of *Pinus sylvestris*. Ecology 75:660-670

Stouraunet, K.O. 2004. Models to predict time since death of *Picea abies* snags. Scand.J.For.Res. 19:250-260

Storaunet, K.O., and J. Rolstad. 2004. How long do Norway spruce snags stand? Evaluating four estimation methods. Can.J.For.Res. 34:376-383

Swetnam, T.W., C.D. Allen, and J.L. Betancourt. 1999. Applied historical ecology: Using the past to manage for the future. Ecol.Apps. 9:1189-1206

Trofymow, J.A, T.R. Moore, B. Titus, C. Prescott, I. Morrison, M. Siltanen, S. Smith, J. Fyles, R. Wein, C. Camire, L. Duschene, L. Kozak, M. Kranbetter, and S. Visser. 2002. Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate. Can.J.For.Res. 32:780-804

Yarranton, M., and G.A. Yarranton. 1975. Demography of a jack pine stand. Can.J.Bot. 53:10-314

Table 3.1. Inflection points for the mortality rate and mortality acceleration trajectories at each study plot, in comparison to those from data in Kenkel et al (1997).

Site	Maximum Mortality Rate (% $year^{-1}$)	Age of Maximum Mortality Rate	Maximum Mortality Acceleration (% $year^{-2}$)	Age of Maximum Mortality Acceleration
Prince Albert – Poor	1.01	51	0.037	29
Prince Albert – Rich	1.01	66	0.030	34
Candle Lake – Rich	1.10	56	0.061	42
Candle Lake – Poor	1.25	56	0.068	41
Flin Flon – Rich	2.26	47	0.141	34
Flin Flon – Poor	3.25	47	0.315	38
Jenpeg – Rich	1.62	45	0.093	30
Jenpeg – Poor	1.83	48	0.100	32
Thompson – Rich	1.17	38	0.077	25
Thompson – Poor	2.09	44	0.188	35
Kenkel et al(1997)	4.42	30	0.525	23

Table 3.2. Snag fall rate and average, median, and 80th percentile of the standing time of snags at each study plot.

Site	N (snags, downed logs)	Snag Fall Rate (trees year^{-1})	Average (years)	Median (years)	80th percentile (years)
Prince Albert – Rich	(11, 6)	0.020	50	35	81
Prince Albert – Poor	(9, 4)	0.014	72	50	115
Candle Lake – Rich	(46 23)	0.015	67	47	108
Candle Lake – Poor	(68, 44)	0.016	63	44	101
Flin Flon – Rich	(12 27)	0.040	25	18	41
Flin Flon – Poor	(20 28)	0.034	29	21	48
Jenpeg – Rich	(5 13)	0.038	27	19	43
Jenpeg – Poor	(8 17)	0.050	20	14	33
Thompson – Rich	(50 28)	0.018	56	39	90
Thompson – Poor	(78, 91)	0.034	30	21	48

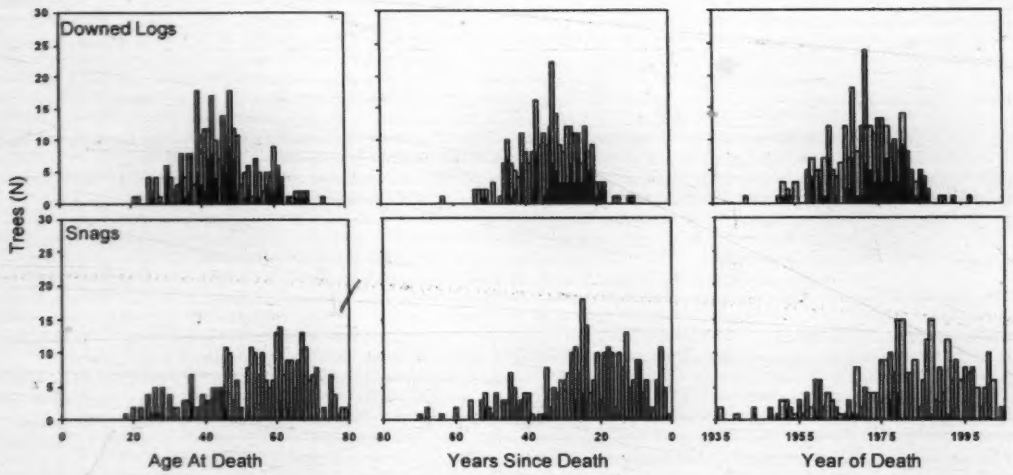

Figure 3.1. Age at death, years since death, and year of death for downed logs (upper charts) and snags (lower charts). Black fill indicates trees for which the year of death was estimated from the 6 trees closest in size. Light grey fill indicates trees where year of death was determined by cross-dating the sample.

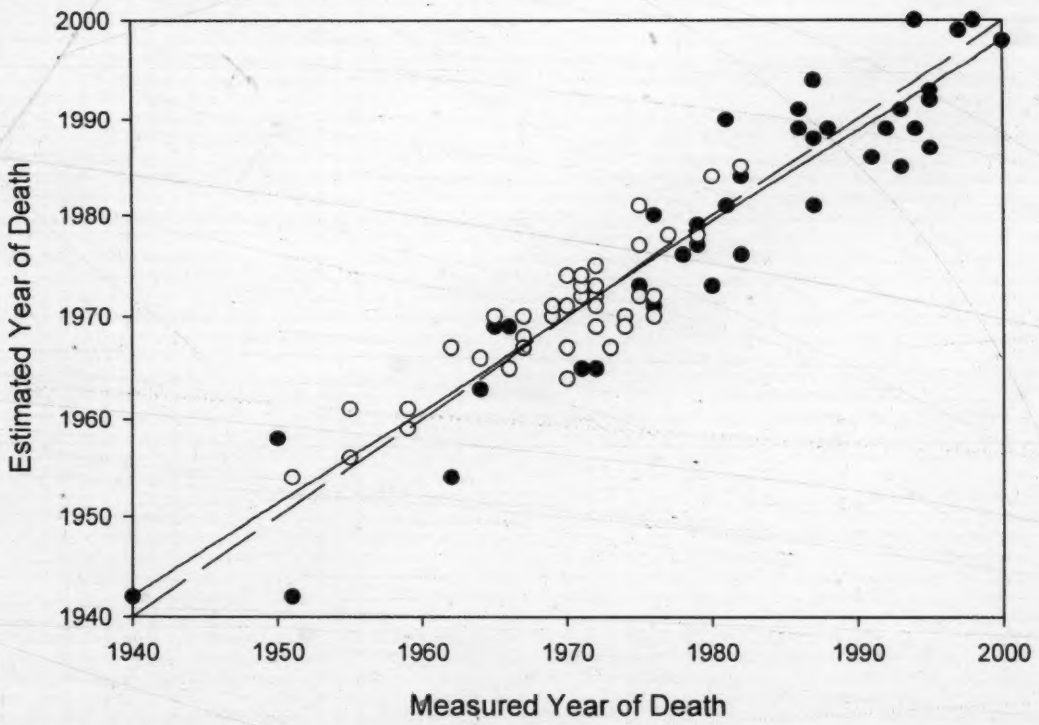

Figure 3.2. The relationship between measured year of death and estimated year of death for trees where year of death was known. Filled circles are snags and empty circles are downed logs. Dashed line is the line of agreement and solid line is the best-fitting linear regression line for all trees.

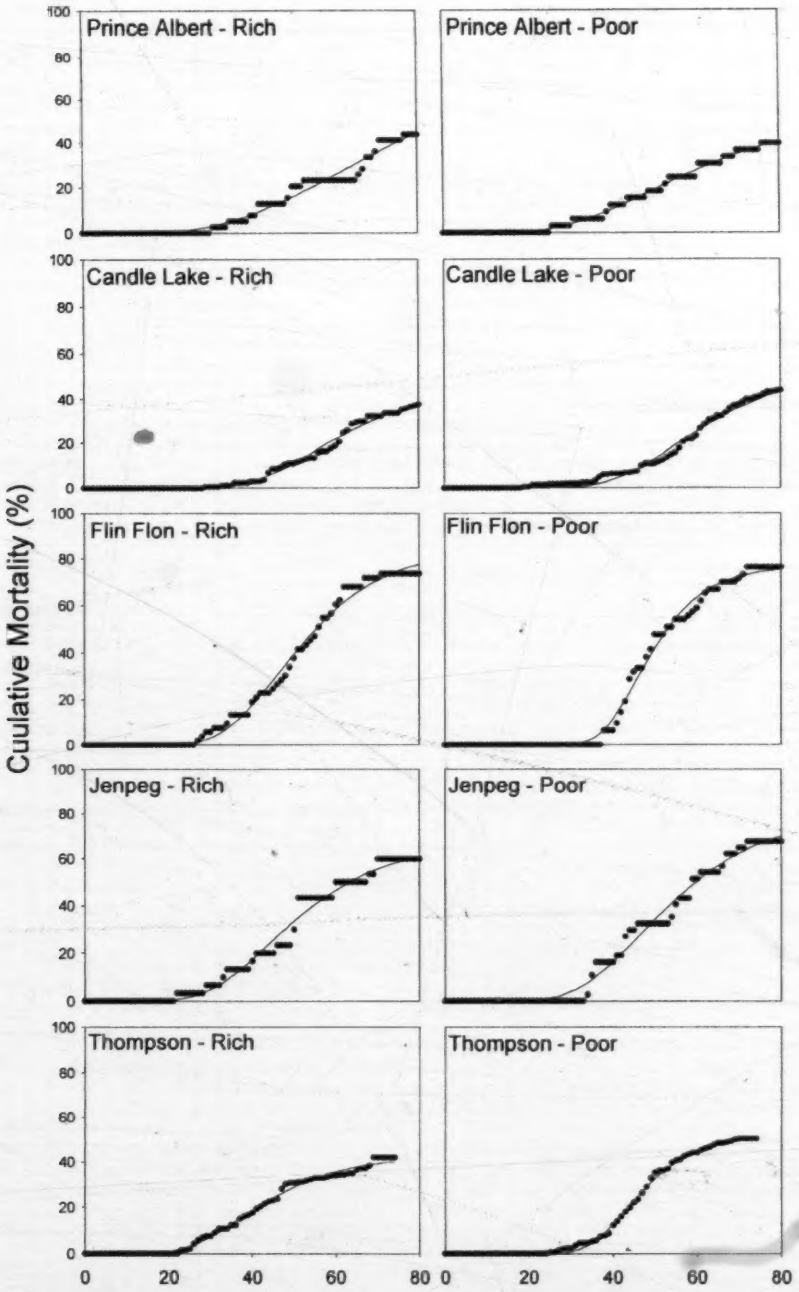

Figure 3.3. The Richards function fit to the cumulative mortality data at each study plot

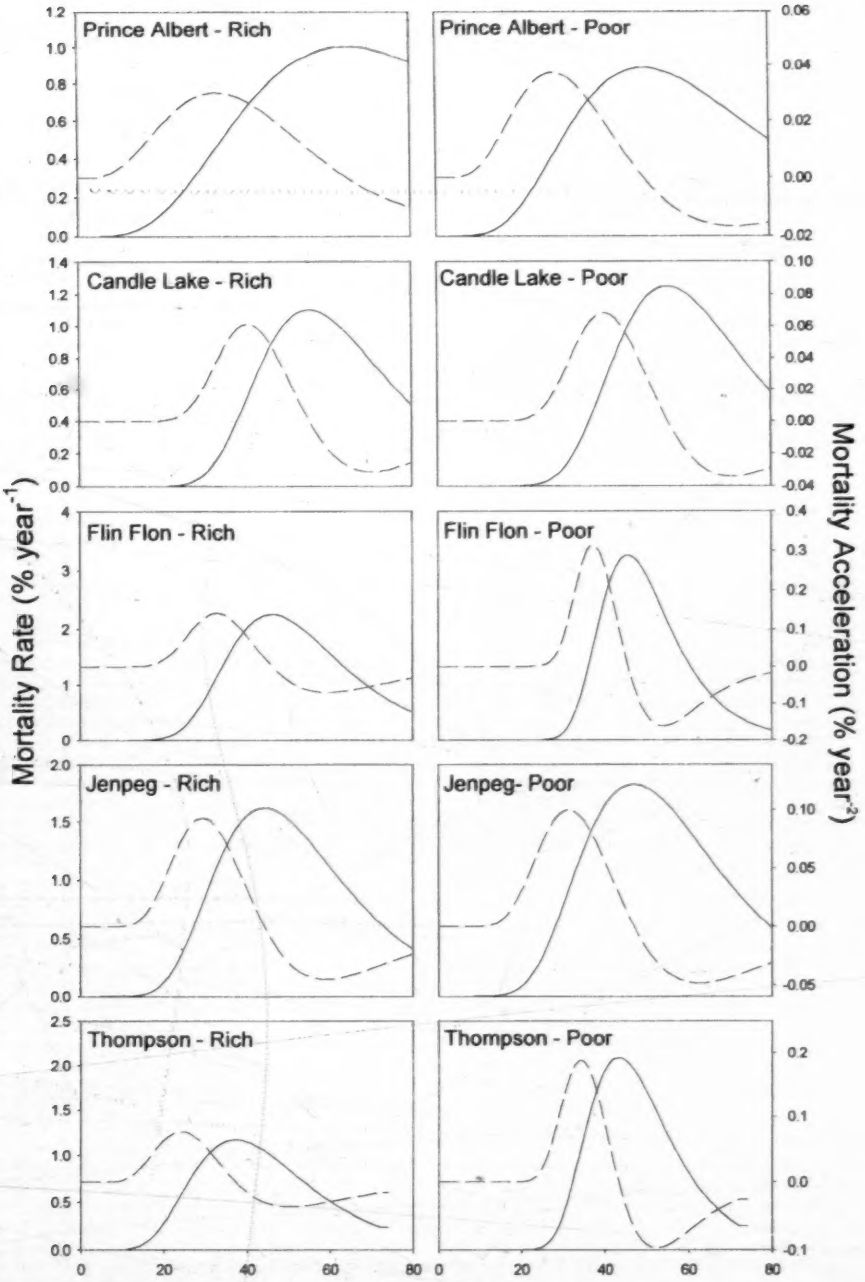

Figure 3.4. Mortality rate (solid line) and acceleration (dashed line) trajectories for each plot based on the 2nd and 3rd derivatives of the Richards function.

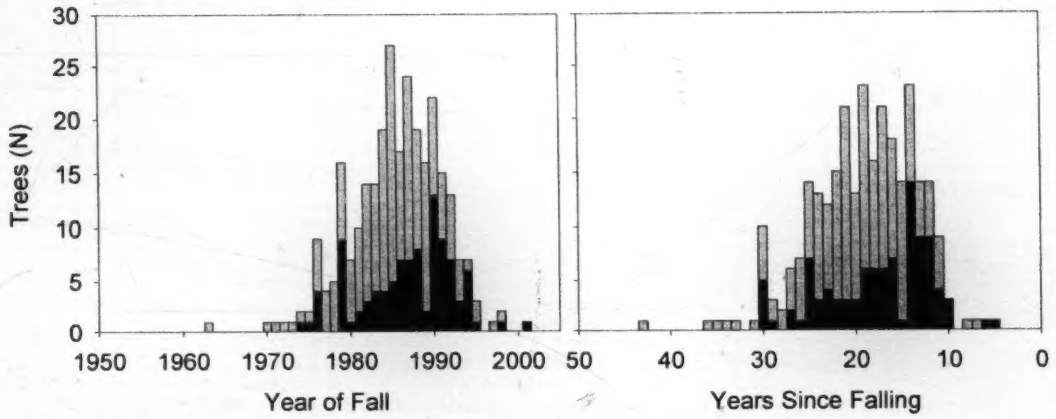

Figure 3.5. Time since falling and year of falling of downed logs. Black areas are trees for which the year of death was estimated from 6 trees closest in size. Light grey areas are trees for which the year of death was directly measured on the samples.

4.0 Using dendrochronology to obtain data for modeling stand development: a substitute for permanent sample plots[1]

Forest growth and stand dynamics models could more easily investigate and account for transient factors like weather variation and defoliation that influence forests at an annual resolution if data monitoring forest growth and stand dynamics were also available at an annual resolution. For Canadian boreal forests, data at this resolution are not presently available. Rather, the vast majority of data presently used to monitor forest growth and stand development are obtained by periodic re-measurement of the breast height diameter, height, and condition of trees at permanent sample plots (PSPs). Plot designs vary by jurisdiction, but re-measurements are typically made at only 5 to 10 year intervals. While periodic re-measurement of PSPs undoubtedly provides accurate estimates of the size and condition of trees at these fixed intervals, it is difficult to use PSP data to determine the effect of transient factors influencing forests at an annual scale because of their coarse temporal resolution. Even if undertaken, yearly re-measurement of PSPs usually cannot obtain annual data because instruments like tapes, calipers, and clinometers used to make field measurements of tree diameters and heights have difficulty resolving the small annual growth increments typical of boreal forests. Further, in regions where PSPs are absent, data from plots established elsewhere must be used to estimate parameters for models used to make local management decisions. Investments made in local PSPs will not return useful monitoring data for a considerable period of time.

Dendrochronology techniques can overcome both of the weaknesses of PSPs. Ring widths measured on increment cores can be resolved annually and can provide detailed time series of diameter growth decades into the past without waiting for PSP re-measurements. For example, Biondi (1999) showed how tree-ring data can be used to obtain insight into stand growth patterns over longer historical periods than is possible using PSPs. Many studies have used tree-ring data to investigate different aspects of forest growth and stand dynamics (e.g. Henry and Swan 1974, Oliver and Stephens 1976, Johnson and Fryer 1989, Stoll et al 1994, Carrer and Urbinati 2001). In this chapter, I show that dendrochronology techniques can be used to retrospectively obtain much of the data that are presently normally acquired by periodically re-measuring PSPs. These data include the spatial and temporal distribution of mortality, tree and stand level volume growth, stand level biomass dynamics, and tree size (diameter) distributions. I also show that the data obtained by these techniques provides more information than the data obtained from periodic re-measurement of PSPs, and that they can quickly obtain long time series of data in areas currently lacking a PSP infrastructure, relative to waiting to observe changes at a PSP established today. The importance of such data will increase in the future as climate change begins to impact the ecological structure and function of boreal forests in Canada (e.g. Hogg and Bernier 2005, Spittlehouse 2005),

---

[1] A version of this chapter has been submitted for publication. Metsaranta, J.M., and Lieffers, V.J. (in review) Using dendrochronology to obtain data for modeling stand development: a substitute for permanent sample plots. Submitted to Forestry

affecting both growth and stand development processes. Monitoring the magnitude and direction of these impacts is important for forest management agencies wishing to adapt management practices to climate change effects.

4.1 Methods

4.1.1 Field and laboratory

I used data from the nutrient rich stem mapped plot located at Candle Lake (refer to chapter 1 for further characteristics of this plot). Field data collection and laboratory sample processing were conducted as described in chapter 1, with the exception of an additional procedure for estimating the ring-widths of excessively decomposed trees. Absence of ring-widths for decomposed trees results in missing data, and an underestimation of total stand growth. As described in chapter 3, I used the breast height diameters of decomposed trees and the mean year of death of the 3 larger and 3 smaller trees nearest in diameter, of the same class (snag or downed log) and at the same plot to estimate the year of death as an estimate of each excessively decomposed tree. I showed this method provides unbiased estimates of year of death, with a mean absolute difference between the measured and estimated year of death of 3.3 (SD 2.4) years. Here, I use the mean ring width from these same 6 trees to estimate the ring widths for each excessively decomposed tree.

4.1.2 Reconstructing mortality

As described in chapter 1, I visually cross-dated samples against a master chronology to account for missing rings on living trees and to determine the year of death for dead trees. At the nutrient rich site at Candle Lake, most samples (94.1%) had the highest correlation at the final assigned date (97.7% for ±1 year). The average correlation with the master chronology at the assigned date was r^2=0.89 (SD=0.09, range=0.76 to 0.98, n=171). For this chapter, I use these data to generate a series of decadal maps of the distribution of live and dead trees at the plot, starting in 1960.

4.1.3 Reconstructing volume

As I showed in chapter 2, the annual diameter (inside bark D_{ib}) of each tree determined from ring-width measurements can be used to accurately estimate cumulative volume and volume increment by partial stem analysis. This required three steps. First, diameter inside bark (D_{ib}) was converted to diameter outside bark (D_{ob}) using (Husch et al 2003):

$$D_{ib} = k\, D_{ob} \tag{4.1}$$

From data in Halliwell and Apps (1997), k was estimated to be 0.964 (95% C.I. 0.961 to 0.966, n=221, r^2=0.99). Heights were estimated from D_{ob} with the Chapman-Richards function:

$$H = 1.3 + a(1 - e^{-b \cdot D_{ob}})^c \tag{4.2}$$

where H is tree height (m), and the parameters a, b, and c were estimated to be a = 18.866 (95% CI 17.541 20.191), b = 0.105 (95% CI 0.079, 0.131), and c = 1.482 (95% CI 0.143 1.820) (n= 392, r^2=0.98, MSE = 3.407), based upon data in Halliwell and Apps (1997), supplemented with data from the current study plots. Volumes were estimated from H and D_{ob} using:

$$D_{ib} = a_0 D_{ob}^{a_1} a2^{D_{ob}} X_i^{b_1 z_i^2 + b_2 \ln(z_i + 0.001) + b_3 \sqrt{z_i} + b_4 e^{z_i} + b_5 (D_{ob}/H)} \quad (4.3)$$

where the components are as defined in Kozak (1988), and parameters were obtained from Gal and Bella (1994) (also see chapter 2). Total volumes were determined using numerical integration. Volume increment was obtained by subtracting volume in year y_{-1} from volume in year y, and was expressed in $m^3 year^{-1}$.

As I also described in chapter 2, these equations were chosen because their parameters could be estimated from easily available data, or obtained from the literature. All of these methods are under constant development by forest mensurationists, so they could all easily be replaced by other equations, particularly if they were sensitive to the effect of stand conditions and competitive effects on height-diameter relationships (e.g. Sharma and Zhang 2004) or tree taper (e.g. Morris and Forslund 1992, Muhairwe et al 1994). Stand level volume and increment were obtained by summing the individual tree values for each year, annual mortality by summing the volume of trees that died in a given year.

4.1.4 Reconstructing biomass

I also reconstructed trajectories for stemwood biomass of living trees, snags, and downed logs. I estimated total stemwood biomass Y (tonnes, including stump and top to an upper limit diameter of 2cm) using

$$Y = a_0 + a_1 D_{ob} + a_2 D_{ob}^2 + a_3 D_{ob}^3 \quad (4.4)$$

with parameters a_0, a_1, a_2, and a_3 obtained from Singh (1982). Biomass increment was determined by subtracting biomass in year y-1 from biomass in year y. Stand level cumulative biomass and annual biomass increment were obtained by summing the individual tree values for each year. Annual biomass mortality was obtained by summing the biomass of trees that died in a given year. Biomass prediction equations are also under constant development. In practice, the equation used could be substituted with one more precisely calibrated to local growth conditions (e.g. Bond-Lamberty et al 2002), or with one that applies more generally to a larger geographic region(e.g. Lambert et al 2005).

Trees that die first become standing snags and then later fall down to become downed logs. I estimated a time of falling for each snag based upon the method described in Gore et al (1985), which uses data on the time since death of standing snags and downed logs to estimate snag fall rates, based on an assumption of exponential fall down rate. By cross-dating, I knew the year of death of both the snags and downed logs,

and so could apply these methods to estimate the fall rate of snags at the study plot. I describe these results in chapter 3. In practice, other methods of estimating the fall-down rate of snags could also be used if they were more appropriate to local stand conditions (e.g. Johnson and Greene 1991, Storaunet and Rolstad 2004).

This allowed me to estimate when a snag fell to the ground and become a downed log, and therefore to know the number of years t that it had been on the ground, and so estimate how much it decomposed since it fell. I used wood decomposition parameters from Trofymow et al (2002) to estimate the decomposition of a downed log t years since it fell, using a natural log transformed simple exponential decay model of the percent mass remaining

$$\ln(MR\%) = a - kt \tag{4.5}$$

I obtained parameters a and k from the nearest study plot (Prince Albert) in Trofymow et al (2002). As in some other studies, I assumed that snag decomposition was negligible (Johnson and Fryer 1989, Boulanger and Sirois 2006). Using these methods, I could plot annual trajectories of stemwood biomass in living trees, snags, and downed logs for the study plot.

4.1.5 Reconstructing diameter distributions

I also determined the tree size distribution of the population from the reconstructed diameters. Forest growth models commonly describe the size structure of a forest stand using a diameter distribution, using various probability distributions for which the parameters can be estimated by several methods. As noted in Garcia (2006), forestry literature databases contain hundreds of references to papers concerning diameter distribution models. In these studies, the Weibull distribution is commonly used because it is very flexible and can fit distributions with a wide variety of shapes and skewness, many methods exist to estimate its parameters, and because the cumulative density function has a closed form (Bailey and Dell 1973, Little 1983, Rennolls et al 1985). The cumulative distribution function of the Weibull distribution is:

$$F(x) = 1 - \exp\left(-\left(\frac{D_{ob} - a}{b}\right)^c\right) \tag{4.6}$$

where, a is the location parameter, b is the scale parameter, and c is the shape parameter. The location parameter *(a)* of the Weibull distribution is related to the size of the smallest tree in the stand. The scale parameter *(b)* is related to the range of tree sizes in the stand. Adding the value of the location and scale parameters estimates the diameter such that about 63% of the trees are smaller. The shape parameter*(c)* is related to the skewness of the size distribution. The Weibull distribution is positively (right) skewed when $1 < c < 3.6$, approximately normal when $c = 3.6$, and increasingly negatively (left) skewed when $c > 3.6$ (Little 1983, Rennolls et al 1985). To demonstrate what is possible with my data, I annually fit a three parameter Weibull distribution to the reconstructed D_{ob} data from

each plot, and plotted the resulting trajectories of inter-annual variation in the parameters *a*, *b*, and *c*.

4.2 Results and Discussion

4.2.1 Spatial and temporal distribution of mortality

A series of decadal maps of the spatial distribution of living and dead trees at ten year intervals starting in 1960 are plotted in Figure 4.1. These data were obtained from samples collected in 2005, and did not require the plot to have been established as a PSP 50 years prior to sampling in order to obtain them. Several studies have investigated the spatial pattern of jack pine in both pure (e.g. Kenkel 1988, Kenkel et al 1997) and mixed (e.g. Little 2002, Béland et al 2003) stands, based either upon snapshots measurements of a single point in time, or periodically obtained PSP data. If desired, my data would allow maps like those in Figure 4.1 to be generated annually. These annual resolution data would be valuable for investigating hypotheses about the effect of competition on spatial pattern, and further exploring the effect of transient factors like drought, insect defoliation, or root rot on how spatial patterns change over time. These are investigated in chapter 7.

4.2.2 Volume growth trajectories

From the resulting series of volume growth data for individual trees, I calculated: (1) incremental annual volume growth (gross and net), (2) cumulative volume growth (gross and net), and (3) volume mortality (incremental and cumulative). In Figure 4.2, I plot these growth series alongside what the data for these series would look like if this plot had been established as a PSP in 1950, and re-measured on a ten year interval up to the present time. The data obtained from tree-ring reconstructions demonstrate significant annual variation in all of the growth measures considered (Figure 4.2). These variations are not evident if the data are summarized at 10-year intervals (Figure 4.2).

I admit that a weakness of the stand-reconstruction approach is that it does not provide data on past height growth, which is needed to estimate volume. Traditionally, missing heights have been predicted using height-diameter regression equations (e.g. Huang et al 1992, Peng et al 2001), which in the simple form that I used here assume that all trees of a given diameter are the same height. The alternatives to this are: (1) to fell the trees for stem analysis (e.g. Duff and Nolan 1953), (2) make repeated annual measurements of heights, or (3) to derive height prediction equations that are sensitive to the effects of stand conditions on height growth (e.g Sharma and Zhang 2004). The first two of these would defeat the purpose of the methods that I describe, because they would require: (1) all the trees at the plot to be felled for destructive and labour intensive stem analysis, increasing the required data collection effort, or (2) waiting for the trees to grow and making measurements in the future, leaving me without data in the present. I did not have data available to parameterize relationships described in the third alternative, but suggest that this is a very promising avenue of future research in this area.

Even with this weakness, I feel that my methods are reasonable. When collecting data for this study, I measured the height of 79 trees twice, on separate days, with a laser

clinometer. The mean absolute difference between the two measurements was 0.79 m (SD=0.68). Full stem analysis data in Varem Sanders and Cambell (1998) show that annual height increment of jack pine trees in this region averages 0.16 m (SD=0.09). Unless my height measurements were exceptionally sloppy, this shows that annual height growth is likely less than the error of presently available height measurement instruments. In other words, even if they were undertaken, repeated annual height measurements would have difficulty resolving annual height increment in these forests. Similar to height, the slow annual growth rate of boreal forests is often within the bounds of measurement error for instruments like tapes and calipers that are normally used to make field measurements of tree diameters. Measurement error is also induced by changing from tapes to calipers when measuring diameter and not placing measurement instruments exactly at breast height or precisely at the same location at each successive measurement. My technique of extracting two randomly oriented increment cores is essentially identical to measuring tree diameter with randomly oriented calipers, where the calipers are placed in precisely the same location each time, and so potentially can eliminate some of these measurement errors, but perhaps also introduce others, particularly related to the shrinkage of samples. As I showed in chapter 2, for a variety of species and volume estimation methods, the error in determining annual volume increment between this method and stem analysis is always less than 10% and usually less than 5%, a level of error that is common in published mensurational studies that compare different measurement methods (e.g. Martin 1984, Biging 1988, Biging and Wensel 1988, Gregoire et al 1990, Figueiredo-Filho and Schaaf 1999).

4.2.3 Biomass growth trajectories

In Figure 4.3, I plot trajectories of cumulative stemwood biomass (tonnes ha^{-1}) in living trees, standing snags, and downed logs in the study site since 1950. I chose to start in 1950 for this example (and also for all subsequent analysis) because, as I showed in chapter 3, it is reasonable to assume that I could detect nearly all the trees that had died in these stands since 1950. Several studies have investigated the biomass dynamics of jack pine forests (e.g. Nalder and Wein 1999, Preston et al 2006, Shaw et al 2006). In addition, snags and downed logs are important for many ecological functions, including nutrient cycling (e.g. Laiho and Prescott 2004), forest carbon dynamics (e.g. Howard et al 2004, Nalder and Wein 2006, Shaw et al 2006, Preston et al 2006), and forest fire behaviour (e.g Nalder et al 1999). As a result, long-term annual data on the dynamics of both living and dead biomass is necessary for many ecological models. The dendrochronological techniques used here allow a full examination of the biomass dynamics of single stands and because of its annual resolution, provide many advantages over data obtained from chronosequence studies of temporary or permanent sample plots in studies of the dynamics and ecological function of living and dead biomass.

4.2.4 Temporal changes in diameter distributions

In Figure 4.4, I plot a series of histograms depicting the size (diameter) distribution of the study plot at ten year intervals since 1960, with the Weibull distribution fit to the data in those years. In Figure 4.5, I plot the annual trajectory of the location parameter a, the scale parameter b, and the shape parameter c of the Weibull distribution fit to the diameter data at the plot since 1950. The location parameter a, and

the scale parameter b generally increase over time (Figure 4.5), though there is annual variation and there are periods of time during which both decrease. The shape parameter c is generally in the range of $1 < c < 3.6$, indicating that this sites has a positively skewed diameter distribution. In many forest growth models based on diameter distribution, future values of the of the Weibull distribution parameters are estimated from stand characteristics like age, density, site index, or mean tree size (e.g. Newton et al 2004, Newton et al 2005, Nord-Larsen and Cao 2006). Just as it is possible to reconstruct past diameters using ring-widths, it would also be possible to reconstruct any of the many stand characteristics used to both develop and validate yield models of individual trees or whole stands. In addition to diameter distribution based growth models, other metrics are also used to summarize characteristics of tree size distributions, and to make inferences about changes in competition processes. Examples of these are the coefficient of skewness, the coefficient of variation, the Gini coefficient, the Lorenz asymmetry coefficient, and the distribution modifying function (Westoby 1982, Weiner and Solbrig 1984, Bendel et al 1989, Schwinning and Weiner 1998, Damgaard and Weiner 2000, Nord-Larsen et al 2006). I investigate annual changes in some of these metrics, in relation to changes in stand development, inter annual variation in growth rate and inter-annual variation in growing conditions in chapter 5 and chapter 6.

4.3 Conclusions

This chapter shows that retrospective dendrochronological reconstruction offers an alternative way to collect data on forest growth and stand development that can provide more information than data collected from long term re-measurements of PSPs. I obtained a complete census of all trees, but for even-aged single species forests, it is also possible to do stand-level reconstructions from only a sample of the largest trees (Osawa et al 2001, Osawa and Abaimov 2001). Software and hardware for measuring ring-widths are readily available. The cost of this infrastructure for tree-ring analysis capabilities is likely no more than that required for GIS analysis capabilities (Biondi 1999), which are a ubiquitous decision support tool. Though more labour intensive in the short-term than PSPs, dendrochronological samples need only be collected once so have no costs associated with plot maintenance and re-measurement. They are also not subject to risks from vandalism, industrial damage or fire after they have been established because the data on past growth have already been collected. While periodic re-measurement of PSPs provides accurate estimates of tree condition and size at fixed intervals, the dendrochronology approach that I report can provide annual resolution data that also follows the fates of individuals over time. These data would allow an improved representation of transient factors such as insect defoliation, drought, climate change or the interaction of these features with competitive processes in forest growth and stand dynamics models, and therefore for these factors to be more easily considered in management plans. Secondly, dendrochronology techniques can quickly provide long time series of data for areas without a PSP infrastructure – compared to long delays if normal PSPs were established today. These techniques should therefore also be of interest in regions that either do not have a PSP infrastructure, or where the present PSP infrastructure has coverage gaps in certain stand types.

4.4 Literature Cited

Bailey, R.L., and T.R. Dell. 1973. Quantifying diameter distributions with the Weibull function. For.Sci. 19:97-104.

Béland, M., J-M Lussier, Y. Bergeron, M-H Longpre, and M. Béland. 2003. Structure, spatial distribution and competition in mixed jack pine (*Pinus banksiana*) stand on clay soils of eastern Canada. Ann.For.Sci. 60:609-617.

Bendel, R.B., S.S. Higgins, J.E. Teberg, and D.A. Pyke. 1989. Comparison of skewness coefficient, coefficient of variation, and Gini coefficient as inequality measures within populations. Oecologia 78:394-400.

Biging, G.S. 1988. Estimating the accuracy of volume equations using taper equations of stem profile. Can.J.For.Res. 18:1002-1007.

Biging, G.S. and L.C. Wensel. 1988. The effect of eccentricity on the estimation of basal area and basal area increment of coniferous trees. For.Sci. 34:621-633.

Biondi, F. 1999. Comparing tree-ring chronologies and repeated timber inventories as forest monitoring tools. Ecol.Appls. 9:216-227.

Bond-Lamberty, B., C. Wang and S.T. Gower. 2002. Aboveground and belowground biomass and sapwood area allometric equations for six boreal tree species of northern Mantioba. Can.J.For.Res. 32:1441-1450

Boulanger, Y., and L. Sirois. 2006. Postfire dynamics of black spruce coarse woody debris in northern boreal forest of Quebec. Can.J.For.Res. 36:1770-1780

Carrer, M., and C. Urbinati. 2001. Spatial analysis of structural and tree-ring related parameters in a timberline forest in the Italian Alps. J.Veg.Sci. 12:643-52.

Damgaard, C. and J. Weiner. 2000. Describing inequality in plant size or fecundity. Ecology 81:1139-1142

Duff, G.H., and N.J. Nolan. 1953. Growth and morphogenesis in the Canadian forest species. I. The controls of cambial and apical activity in *Pinus resinosa*. Can.J.Bot. 31:471–513.

Figueiredo-Filho, A. and L.B. Schaaf. 1999. Comparison between predicted volumes estimated by taper equations and true volumes obtained by the water displacement technique (xylometer). Can.J.For.Res. 29:451-461.

Gál, J., and I.E. Bella. 1994. New stem taper functions for 12 Saskatchewan timber species. Nat.Res.Can., Can.For.Serv., North.For.Cent., Edmonton, AB. Inf.Rep. NOR-X-338

Garcia, O. 2006. Scale and spatial structure effects on tree size distributions: implications for growth and yield modeling. Can.J.For.Res. 36:2983-2993

Gore, A.P., E.A. Johnson and H.P. Lo. 1985. Estimating the time a dead tree has been on the ground. Ecology 66:1981-1983

Gregoire, T.G., S.M. Zedaker, and N.S. Nicholas. 1990. Modeling relative error in stem basal area estimates. Can.J.For.Res. 20:496-502.

Halliwell, D.H., and M.J. Apps. 1997. Boreal Ecosystem-Atmosphere Study (BOREAS) biometry and auxiliary sites: overstory and understory data. Nat.Res.Can., Can.For.Serv., North.For.Cent., Edmonton, AB.

Henry, J.D., and J.M.A Swan. 1974. Reconstructing forest history from live and dead plant material – an approach to the study of forest succession in southwest New Hampshire. Ecology 55:772-783.

Hogg, E.H., and P.Y. Bernier. 2005. Climate change impacts on drought-prone forests in western Canada. For.Chron. 81:675-682

Huang, S., S.J. Titus, and D. Wiens. 1992. Comparison of nonlinear height-diameter functions for major Alberta tree species. Can.J.For.Res. 22:1297-1304.

Husch, B, T.W. Beers., and J.A. Kershaw. 2003. Forest Mensuration, 4th Ed. John Wiley and Sons, Hoboken, NJ.

Howard, E.A., S.T. Gower, J.A. Foley, and C.J. Kucharik. 2004. Effects of logging on carbon dynamics of a jack pine forest in Saskatchewan, Canada. Glob.Change Biol. 10:1267-1284

Johnson, E.A., and G.I. Fryer. 1989. Population dynamics in lodgepole pine-engelmann spruce forests. Ecology 70:1335-1345.

Johnson, E.A., and D.F. Greene. 1991. A method for studying dead bole dynamics in Pinus contorta var. latifolia - Picea engelmanii forests. J.Veg.Sci. 2:523-530

Kenkel, N.C. 1988. Patterns of self-thinning in jack pine: testing the random mortality hypothesis. Ecology 69:1017-1024.

Kenkel, N.C., M.L. Hendrie and I.E. Bella. 1997. A long-term study of *Pinus banksiana* population dynamics. J.Veg.Sci. 8:241-254.

Kozak, A. 1988. A variable-exponent taper equation. Can.J.For.Res. 18:1362-1368.

Laiho, R., and C.E. Prescott. 2004. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. Can.J.For.Res. 34:763-777

Lambert, M-C., C-H. Ung, and F. Raulier. 2005. Canadian national tree aboveground biomass equations. Can.J.For.Res. 35:1996-2018.

Little, S.N. 1983. Weibull diameter distributions for mixed stands of western conifers. Can.J.For.Res. 13:85-88.

Little, L.R. 2002. Investigating competitive interactions from spatial patterns of trees in multi-species boreal forests: the random mortality hypothesis revisited. Can.J.Bot. 80:93-100.

Martin, A.J. 1984. Testing volume equation accuracy with water displacement techniques. For.Sci. 30:41-50.

Morris, D.M., and R.R. Forslund. 1992. The relative importance of competition, microsite, and climate in controlling the stem taper and profile shape in jack pine. Can.J.For.Res. 22:1999-2003

Muirhawe, C.K., V.M. LeMay and A. Kozak. 1994. Effects of adding tree, stand, and site variables to Kozak's variable-exponent taper equation. Can.J.For.Res. 24:252-259.

Nalder, I.A., R.W. Wein, M.E. Alexander and W.J. de Groot. 1999. Physical properties of dead and downed round-wood fuels in the boreal forests of western and northern Canada. Int.J.Wild.Fire. 9:85-99

Nalder, I.A., and R.W. Wein. 1999. Long-term forest floor carbon dynamics after fire in upland boreal forests of western Canada. Glob.Biogeochem.Cycles 13:951-968.

Nalder, I.A., and R.W. Wein. 2006. A model for the investigation of long-term carbon dynamics in boreal forests of western Canada I. Model development and validation. Ecol.Mod. 192:37-66.

Newton, P.F., Y. Lei and S.Y. Zhang. 2004. A parameter recovery model for estimating black spruce diameter distributions within the context of a stand density management diagram. For.Chron. 80:349-358.

Newton, P.F., Y. Lei and S.Y. Zhang. 2005. Stand-level diameter distribution yield model for black spruce plantations. For.Ecol.Man. 209:181-192.

Nord-Larsen, T., and Q.V. Cao. 2006. A diameter distribution model for even-aged beech in Denmark. For.Ecol.Man. 231:218-225.

Nord-Larsen, T., Damgaard, C., and Weiner, J. 2006. Quantifying size-asymmetric growth among individual beech trees. Can.J.For.Res. 36:418-425

Oliver, C.D., and E.P. Stephens. 1978. Reconstruction of a mixed-species forest in Central New England. Ecology 58:562-572.

Osawa, A. and A.P. Abaimov. 2001. Feasibility of estimating stem size distribution from measurement on the largest trees in even-aged pure stands. Can.J.For.Res. 31:910-918.

Osawa, A., A.P. Abaimov, and T. Kajimoto. 2001. Feasibility of estimating total stem volume and aboveground biomass from measurement on the largest trees in even-aged pure stands. Can.J.For.Res. 31:2042-2048.

Peng, C., L. Zhang and J. Liu. 2001. Developing and validating nonlinear height-diameter models for major tree species of Ontario's boreal forests. N.J.App.For. 18:87-94.

Preston, C.M., J.S. Bhatti, L.B. Flanagan, and C. Norris. 2006. Stocks, chemistry, and sensitivity to climate change of dead organic matter along the Canadian boreal forest transect case study. Clim.Change 74:223-251.

Rennolls, K., D.N. Geary and T.J.D. Rollinson. 1985. Characterizing diameter distributions by the use of the Weibull distribution. Forestry 58:57-66.

Schwinning, S, and J. Weiner. 1998. Mechanisms determining the degree of size symmetry in competition among plants. Oecologia 113:447-455

Sharma, M., and S.Y. Zhang. 2004. Height-diameter models using stand characteristics for Pinus banksiana and Picea mariana. Scand.J.For.Res. 19:442-451.

Shaw, C., O. Chertov, A. Komarov, J. Bhatti, M. Nadporozskaya, M. Apps, S. Bykhovets and A. Mikhailov. 2006. Application of the forest ecosystem model EFIMOD 2 to jack pine along the Boreal Forest Transect Case Study. Can.J.Soil Sci. 86:171-185

Singh, T. 1982. Biomass equations for ten major tree species of the prairie provinces. Env.Can., Can.For.Serv., North.For.Cent. Edmonton, AB. Inf.Rep. NOR-X-242

Stoll, P., J. Weiner and B. Schmid. 1994. Growth variation in a naturally established population of *Pinus sylvestris*. Ecology 75:660-670.

Storaunet, K.O., and J. Rolstad. 2004. How long do Norway spruce snags stand? Evaluating four estimation methods. Can.J.For.Res. 34:376-383

Spittlehouse, D. 2005. Integrating climate change adaptation into forest management. For.Chron. 81:691-695

Trofymow, J.A, T.R. Moore, B. Titus, C. Prescott, I. Morrison, M. Siltanen, S. Smith, J. Fyles, R, Wein, C. Camire, L. Duschene, L. Kozak, M. Kranbetter and S. Visser. 2002. Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate. Can.J.For.Res. 32:780-804.

Varem-Sanders, T.M.L., and I.D. Campbell. 1998. Boreal Ecosystem-Atmosphere study (BOREAS) biometry and auxiliary sites: X-ray densitometry of tree allometry samples. Nat.Res.Can., Can.For.Serv., North For.Cent., Edmonton, AB.

Weiner, J. and O.T. Solbrig. 1984. The meaning and measurement of size hierarchies in plant populations. Oecologia 61:334-336.

Westoby, M. 1982. Frequency distributions of plant size during competitive growth of stands: the operation of distribution modifying functions. Ann.Bot. 50:733-735.

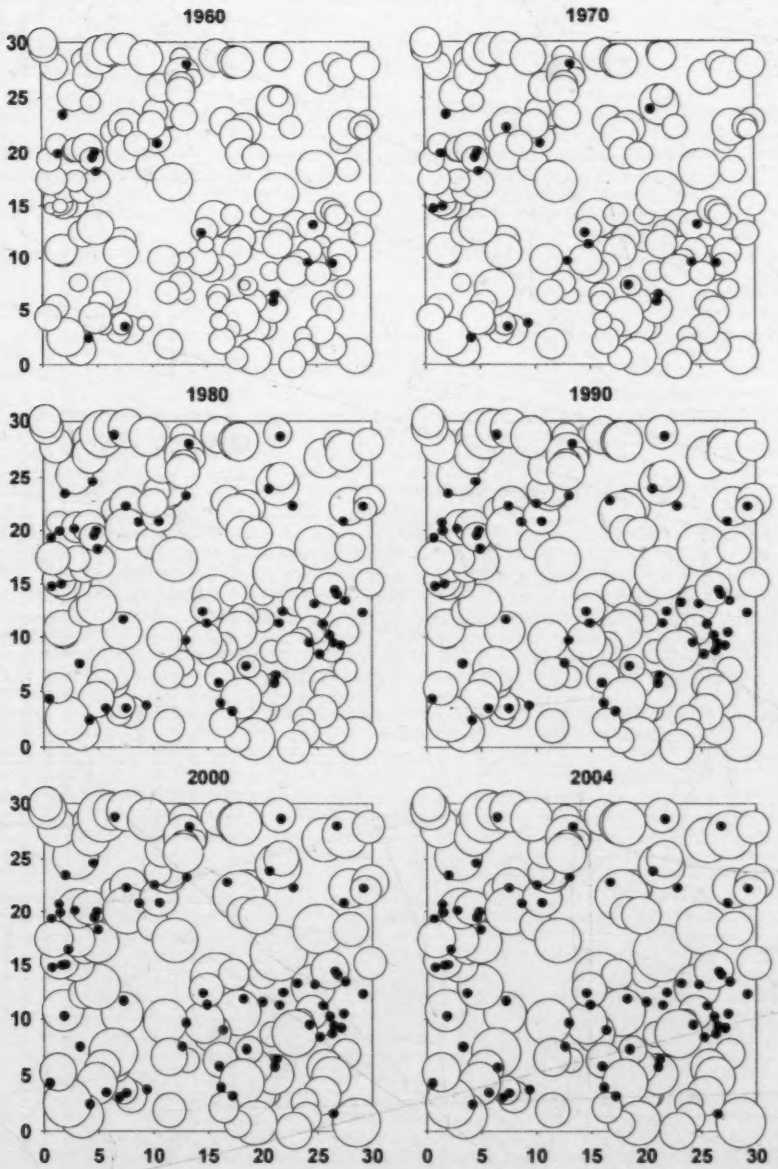

Figure 4.1. A series of decadal maps of live (empty circles with size proportional to DBH) and dead (dark circles) trees since 1960 at the rich site at Candle Lake, determined by cross-dating the year of death of standing and downed dead trees found at the plot in 2005.

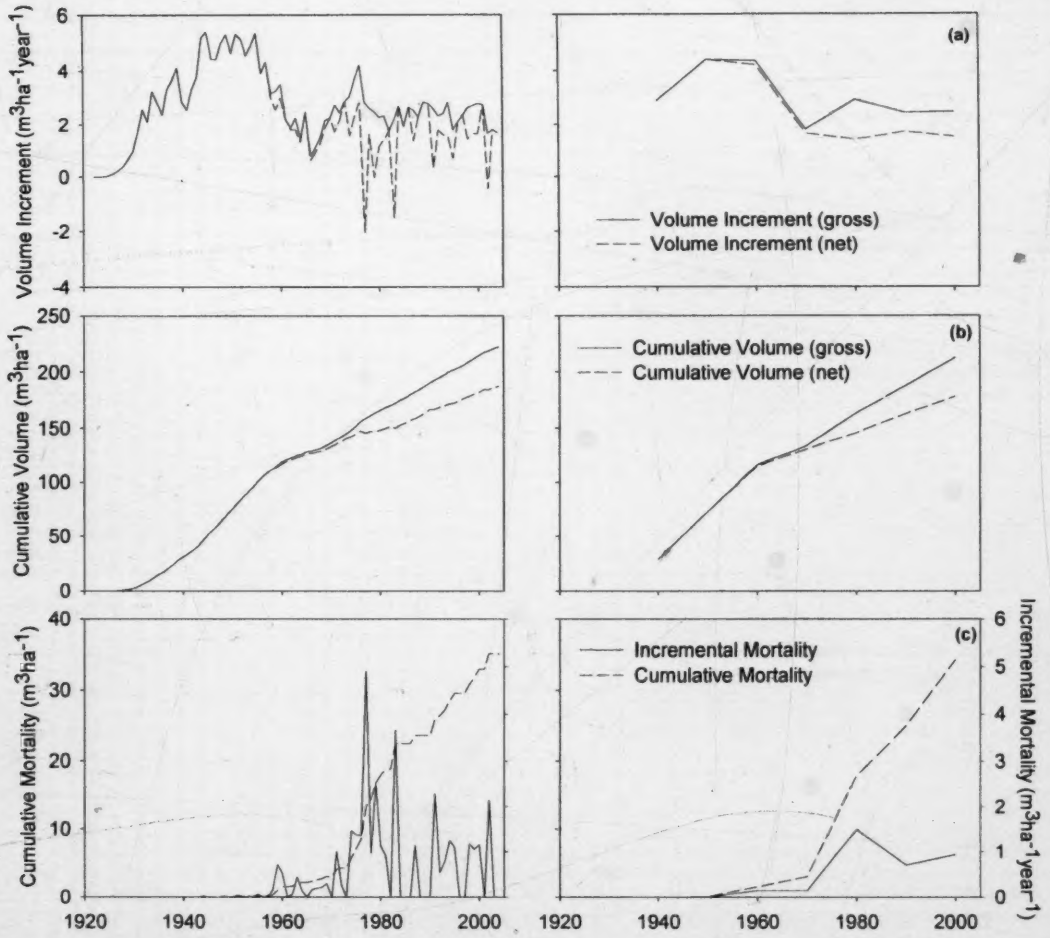

Figure 4.2. On the left are the patterns of growth for the rich site at Candle Lake, determined from full stand reconstruction. On the right is what would be known about these patterns if a PSP had been established at the site in 1950 and re-measured every 10 years. The growth series plotted include (a) incremental volume growth (gross and net), (b) cumulative volume growth (gross and net), and (c) volume mortality (incremental and cumulative).

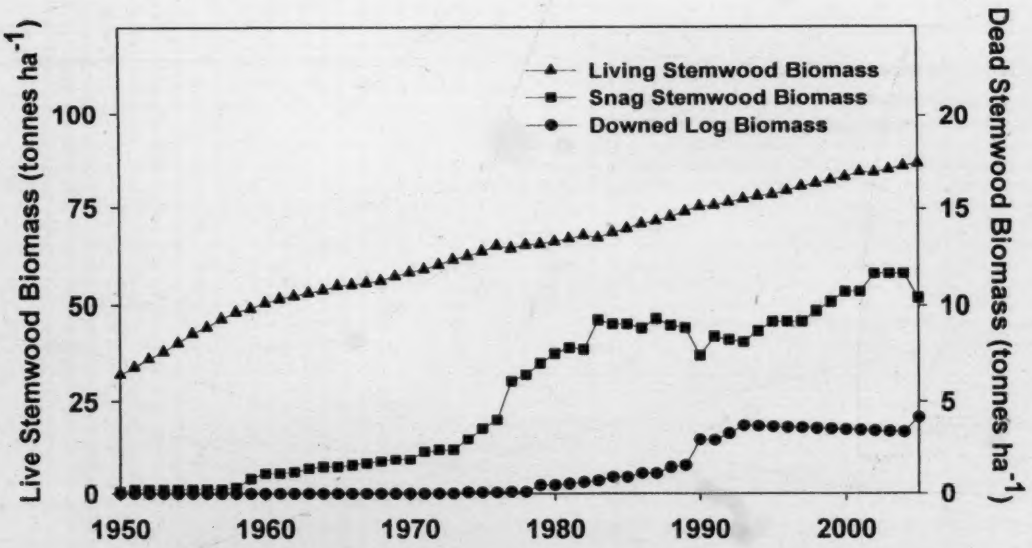

Figure 4.3. Trajectories of stemwood biomass (tonnes ha^{-1}) in living trees, standing snags, and downed logs at the rich site at Candle Lake, calculated from a complete ring-width reconstruction of all living and dead trees, using biomass equations, estimates of the fall down rate of snags, and estimates of the decomposition rate of downed logs.

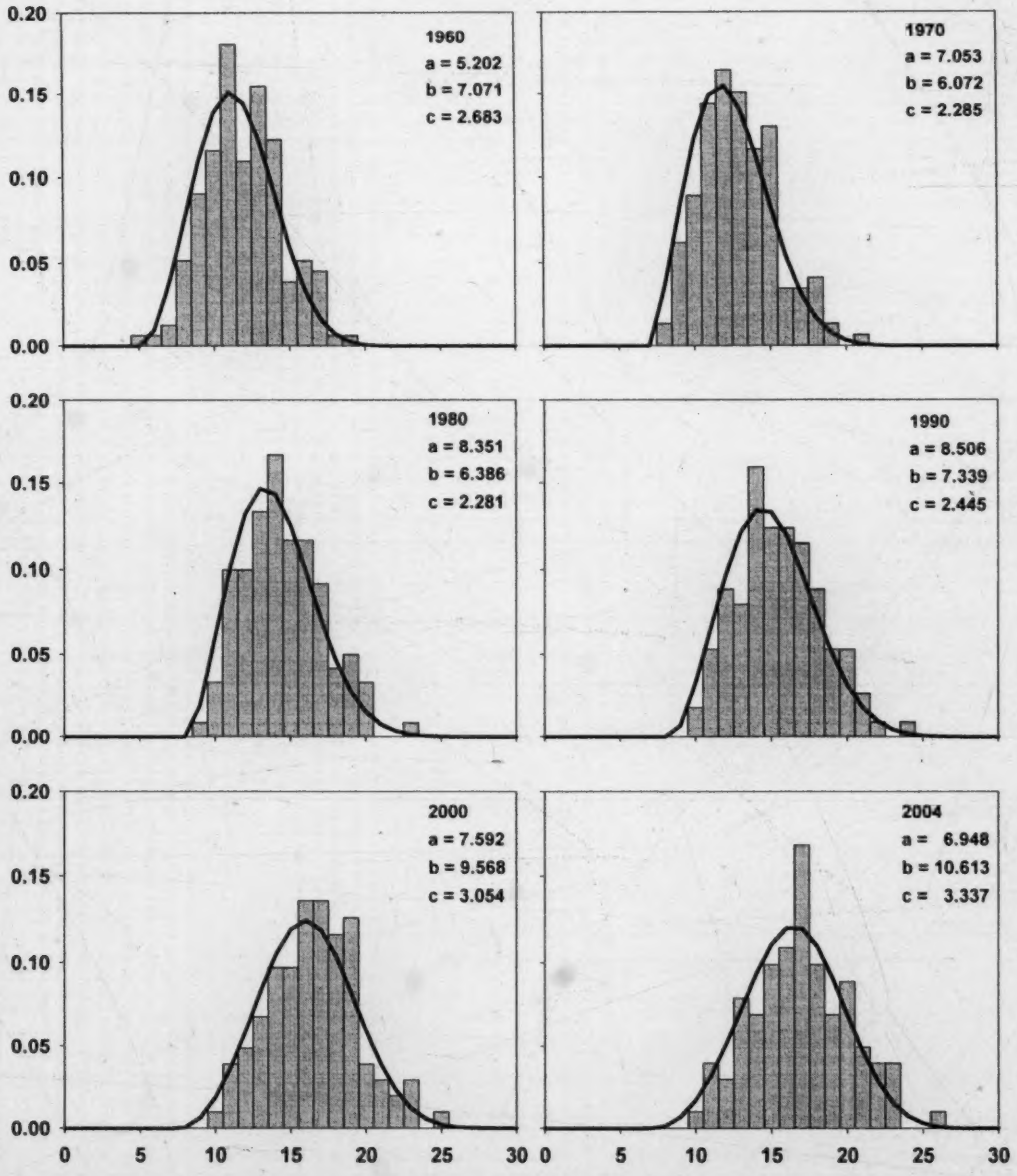

Figure 4.4. A series of decadal histograms of the diameter distribution since 1960 for the rich site at Candle Lake, based on diameter data obtained from a complete ring-width reconstruction of all living and dead trees. The solid line represents the Weibull distribution, fit to the diameter data in each depicted year.

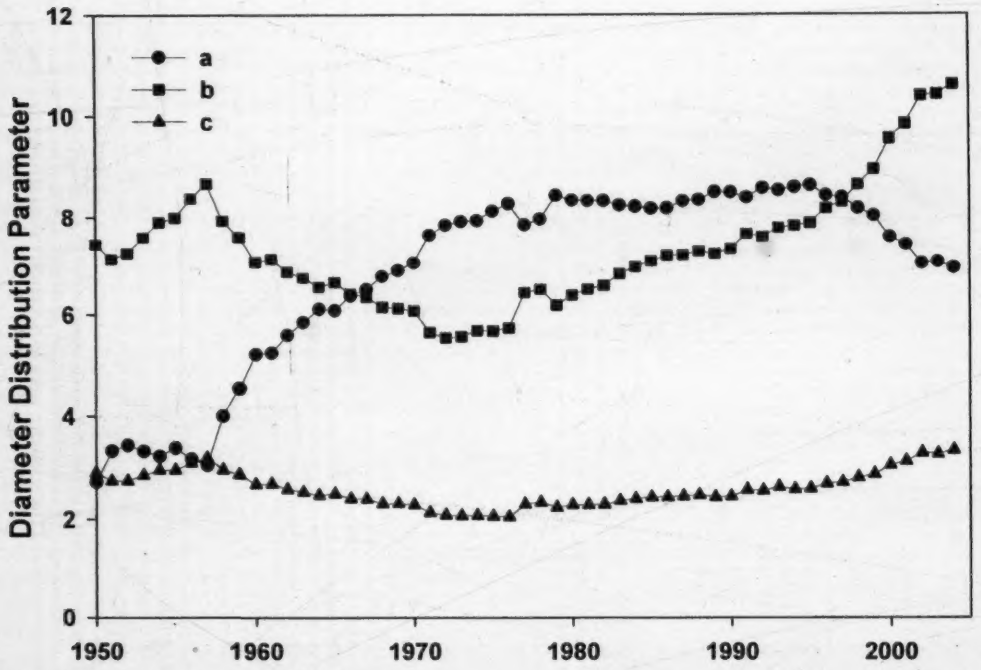

Figure 4.5. Annual trajectories of the location (a), scale (b), and shape (c) parameters of the Weibull distribution, fit to diameter distribution data each year since 1950 for the rich site at Candle Lake, based on diameter data obtained from a complete ring-width reconstruction of all living and dead trees.

5.0 Inequality of size and size increment in *Pinus banksiana* in relation to stand dynamics and annual growth rate[1]

Size variability in plant populations may be due to differences in competitive status, genetics, the differential effects of herbivores and pathogens (Weiner and Thomas 1986), or to spatial and temporal environmental heterogeneity (Schwinning and Weiner 1998, Wichmann 2001). In tree populations, size variability also contributes to the structural diversity of a forest stand, which is important for many ecological functions (Brassard and Chen 2006). Studies of size variability in tree populations have focused mainly on fitting various probability distribution functions to size (diameter) distributions, (as noted in Garcia (2006), there are hundreds of papers concerning diameter distribution models in forestry literature databases). However, size variability in tree populations can also be described as a size hierarchy, and so can be described by other characteristics like its degree of size inequality (Weiner and Solbrig 1984). Changes in size inequality are often attributed to changes in the mode of competition during different stages of stand development (e.g. Gates et al 1983, Weiner and Thomas 1986, Newton and Smith 1988, Kenkel et al 1997). Previous studies have observed that inequality is greater at higher densities (Brand and Magnussen 1988, Knox et al 1989), increases prior to self-thinning and decreases as self-thinning progresses (Mohler et al 1978, Knox et al 1989). In addition, though previous studies have examined the relationship between size and size increment (also known as the distribution modifying function (Westoby 1982, Weiner 1990, Weiner and Damgaard 2006), there has been little attention put on examining the inequality of size increment itself.

Inter-tree competition is considered either a resource pre-emption (size asymmetric) process or a resource depletion (size symmetric) process. Immediately after stand initiation, individual trees are small in comparison to their relative density, so if competition exists at all, its mode is symmetric. Over time, as trees grow larger and a size hierarchy begins to develop, the mode of competition is thought to become asymmetric as larger trees pre-empt light from smaller trees. Tree size at any given point contains a 'memory' of the processes that influenced that individual as it grew from a smaller size, and therefore changes in the inequality of tree size should be best explained by long-term changes in stand characteristics like density, mean tree size, and the average amount of competition. In contrast, the size increment of individual trees varies greatly from year to year, in response to transient factors like annual variation in weather and insect defoliation (e.g. Larsen and MacDonald 1995, Brooks et al 1998, Hofgaard et al 1999, Hogg et al 2005, Hogg and Wein 2005). These factors may have different effects on large and small individuals (Orwig and Abrams 1997, Piutti and Cescatti 1997, Wichmann 2001). Therefore, the inequality of size increment may be more strongly related to annual variation in stand level growth rate, which can be considered a surrogate variable accounting for the transient environmental factors affecting a stand. The

---

[1] A version of this chapter has been published. Metsaranta, J.M., and Lieffers, V.J. 2007. Inequality of Size and Size Increment in *Pinus banksiana* in Relation to Stand Dynamics and Annual Growth Rate. Annals of Botany. doi:10.1093/aob/mcm320

influence of these transient factors on the mode of competition between plants requires further study (Schwinning and Weiner 1998).

In this chapter, I use detailed growth data obtained from tree-ring reconstruction to study annual changes in the inequality of size and size increment at four even-aged fire origin jack pine (*Pinus banksiana* Lamb.) stands. When combined with cross-dating of recent and historical mortality, tree-ring reconstruction can obtain annual data on the size and growth rate of individual trees (e.g. Henry and Swan 1974, Oliver and Stephens 1976, Johnson and Fryer 1989, Stoll et al 1994, Carrer and Urbinati 2001). Though intensive to collect, these data can be advantageous because they follow the growth and mortality of individuals over time (Weiner 1995) and are at an annual resolution. I hypothesize that at any given time, tree sizes are more equal than tree size increments, and that annual trends in inequality will be more variable for size increment than for size. I also hypothesize that, because sizes change slowly, the inequality of tree sizes will be best predicted by long term changes in stand population parameters like stand density, mean tree size, and the average amount of competition. In contrast, because the inequality of tree size increment is more variable, I hypothesize that it will be best predicted by short term population parameters like stand level annual growth increment.

5.1 Methods

5.1.1 Field and laboratory

Field data collection and laboratory sample processing were conducted as described in chapter 1. Ring-widths were converted to volume as described in chapter 2 and again in chapter 4. In this chapter, I only use data from the 900 m^2 plots at Thompson and Candle Lake because calculation of the amount of competition that each tree is subject to requires spatial data.

5.1.2 Determining competition

I determined the level of competition each tree was subject to over time by annually determining a distance-weighted absolute size index of competition for each tree. The index is similar to Hegyi's (1974) relative size index, but uses the absolute size of competitors rather than weighting them by the size of the subject tree. The absolute size of competitors may be a better measure of competition than relative size (Ramseier and Weiner 2006). The index was calculated as

$$C_i = \sum_{j=1}^{N_i} D_j \cdot \frac{1}{d_{ij}} \tag{5.1}$$

where C_i is the index for subject tree i, D_j is the diameter of competitor j, d_{ij} is the distance between subject tree i and competitor j, and N_i is the number of competitors for subject tree i. As trees grow, the definition of which trees compete with each other changes, so I made the competitor search radius for each tree temporally variable based upon an estimate of its crown width. I estimated crown width from diameter using

$$W = a\,D^b \tag{5.2}$$

where W is crown width (m) and D diameter (cm). From data in Halliwell and Apps (1997), I estimated the parameters to be $a = 0.353$ and $b = 0.682$ (n=235, r^2=0.69). I defined the search radius for competitors as 3.5 times the crown width in a given year (Lorimer 1983), and calculated the index only for those trees where the search radius did not fall outside of the plot. At each site, I calculated the average amount of competition trees at each plot were subject to in each year, and used this as a predictor of the trends in size and size increment inequality. To help interpret competition effects, I also determined trends in the variability of competition that trees at each site were subject to by calculating the coefficient of variation (CV%) of the competition index.

5.1.3 Describing inequality

I used the Gini coefficient (Weiner and Solbrig 1984) to describe annual changes in the inequality of size and size increment. I also calculated annual changes in the Lorenz asymmetry coefficient to establish whether the observed trends in inequality are primarily due to large or small trees (Damgaard and Weiner 2000). The Gini coefficient is the difference between the sample Lorenz curve and the line of perfect equality, where the Lorenz curve is a plot of the cumulative number of individuals (x-axis) is plotted against the cumulative proportion of their total size (y-axis). The Gini coefficient ranges from 0 to 1, where 0 indicates perfect equality (the size or growth of all individuals is the same, or the amount of competition each tree is subject to is the same) and 1 indicates perfect inequality (one tree contains all of the size or growth). It can be calculated from data ordered by increasing size as (Dixon et al 1987)

$$G = \frac{\sum_{i=1}^{n}(2i - n - 1)x_i'}{n^2 \mu} \tag{5.3}$$

The Lorenz asymmetry coefficient (S) summarizes the degree of asymmetry in a Lorenz curve. This is important because populations with different Lorenz curves can have the same Gini coefficient, depending on whether most of the inequality is due to large or small individuals (Weiner and Solbrig 1984). The Lorenz asymmetry coefficient is defined as the point at which the slope of the Lorenz curve is parallel to the line of equality. It is defined as

$$S = F(\hat{\mu}) + L(\hat{\mu}) \tag{5.4}$$

and is calculated using the following three equations from Damgaard and Weiner (2000)

$$\delta = \frac{\hat{\mu} - x_m'}{x_{m+1}' - x_m'} \tag{5.5}$$

$$F(\hat{\mu}) = \frac{m + \delta}{n} \tag{5.6}$$

$$L(\hat{\mu}) = \frac{L_m + \delta x'_{m+1}}{Ln} \quad (5.7)$$

When S>1, the inequality present is due mostly to a small number of very large individuals. When S<1, the inequality present is due mostly to a large number of very small individuals. I calculated both coefficients and 95% confidence intervals from 1000 bootstrap samples (Dixon et al 1987) for each set of annual data on size and size increment at each plot.

5.1.4 Data analysis

I examined how changes in the inequality of size and size increment over time are affected by long term population parameters (age, stand density, and competition) and short term population parameters (stand level annual volume increment). I modeled the temporal development of the Gini coefficients for volume and volume increment at each site using stand density (DENS), mean tree volume (SIZE), the average competition index (COMP), stand level annual volume increment in the current year (AVI), and one year previously (AVI1) as predictor variables. I used multiple linear regression to estimate the parameters and to determine the significance of each of these variables as predictors of annual changes in size and size increment inequality. I used the LM function in the STATS package for the R Statistical System (R Development Core Team 2007) to perform these calculations. Since the data were time series, I examined the potential confounding effects of serial autocorrelation by using generalized least squares to estimate the parameters with the GLS function in the NLME package (Pinheiro et al 2007) for R, assuming that the residuals followed a first order autoregressive (AR1) error structure. The parameter estimates obtained by GLS were not substantially different from those obtained by ordinary least squares, so only the results obtained by OLS are presented. In general, I expected that stand density, mean tree size and average competition would be significant predictors of changes in both size and size increment inequality. I also expected that stand level annual volume increment would be a significant predictor of inequality of size increment, but would not be a significant predictor of inequality of size.

5.2 Results

5.2.1 Size and growth rate inequality

From 1950 to 2004, the Gini coefficient for size was nearly always less than 0.5, meaning that tree sizes could be characterized as equal (Figure 5.1). During the same time period, the Gini coefficient for size increment was also generally less than 0.5, but there were periods at all sites when it was greater than 0.5, indicating that size increment could often be considered more unequal than equal (Figure 5.1). Size inequality generally declined over time. Based upon the 95% confidence intervals, the nutrient poor sites had more unequal tree sizes. Size increment was more unequal than size, and its inequality was also more variable from year to year than inequality in size, showing both increasing and decreasing trends from year to year, depending upon the site. Inequality in size increment was not different at rich and poor sites.

The Lorenz asymmetry coefficient for size increment was also more variable from year to year than the Lorenz asymmetry coefficient for size (Figure 5.2). For the vast majority of time, the Lorenz asymmetry coefficient for size was not significantly different from one, indicating that the observed inequality in tree size was not due to either large or small trees. The Lorenz asymmetry coefficient for size increment, however, had many periods of time when it was significantly less than one at all sites, indicating that the observed inequality in size increments was often due to larger numbers of trees with small size increments. There was one clear exception to this trend. At the rich site at Candle Lake, the two years (1966 and 1967) with Lorenz asymmetry coefficients greater than one correspond to the years with the lowest growth rate at that site, and also to two years during which the historical records of the Canadian Forest Insect and Disease Survey indicate that this area was subject to a jack pine budworm defoliation event. In this specific case, the observed inequality in growth rates at this stand was due to a small number of trees that had high growth rates, most likely because they were not defoliated and continued to grow at a normal rate. However, this analysis could not determine if the trees that maintained larger growth rates were large or small trees.

5.2.2 Average competition and competition variability

The average amount of competition (standardized by the maximum average annual competition observed at a given site so that each plot could be compared on the same scale) showed both increasing and decreasing trends over time at each plot (Figure 5.3). Initially, average competition increased at each site up to about 1970 (Figure 5.3). After that point, it stayed relatively constant at the nutrient rich sites, while the nutrient poor sites showed a second increase in average competition that started about 15 years later (circa 1985). Overall, the increase in average competition from its minimum value was higher at nutrient poor sites (where the minimum value was 0.4 to 0.6 times the maximum) than nutrient rich sites (where the minimum value was 0.7 to 0.8 times the maximum. The coefficient of variation (CV%) for competition ranged from 20% to 50% at all sites (Figure 5.3), indicating that even though the average amount of competition trees were subject to changed over time, the amount each tree was subject to in a given year tended be similar. In addition, although there were periods of time at each site where the CV% for competition had small increasing or decreasing trends, the value of the CV% at any given site only ranged in the order of ±10% over the whole study period, indicating that the variability in the amount of competition that trees were subject to did not change substantially over time.

5.2.3 Regression model results

Size inequality was well described by long-term changes in stand dynamics. With the exception of the rich site at Thompson, density, mean tree size, and average competition were significant predictors of size inequality at all four sites (Table 5.1). At three of the four sites, size inequality was positively associated with density and mean tree size, and negatively associated with average competition. At the poor site at Thompson, size inequality was negatively associated with all three predictors. Only at the rich site at Candle Lake was stand level annual volume increment (in this case, lagged

by one year) a significant predictor of changes in size inequality. Variability in the significance and sign of the coefficients associated with the predictor variables indicates that to some extent the specific relationships between these predictors and changes in inequality were site specific.

Some combination of density, mean tree size, and average competition were also significantly associated with of changes in the inequality of size increment at all but the rich site at Candle Lake, where only stand level annual volume increment (in this case lagged by one year) was a significant predictor (Table 5.1). Again, the sign and significance of the coefficients for these predictors varied, indicating that the specific relationship between them and changes in the inequality of growth rate were also site specific. Stand level annual volume increment was a significant predictor of changes in the inequality of size increment at all four sites. At Candle Lake, the significant predictor was lagged by one year, while at Thompson it was not. In all cases, the sign of the coefficients for this predictor (significant or not) were negative, indicating increasing inequality in volume increment when stand growth rates were low. Figure 5.4 plots the relationship between the inequality of size increment and variation in the stand level annual volume increment to demonstrate this relationship graphically.

5.3 Discussion

Overall, these results showed that factors influencing the annual growth rate of the stand in a given year were also influencing the inequality in growth rates for individual trees in that year. The inequality in size increment was higher in years with poor growth, indicating that it was the years with poor growth that contributed most to the generation of the size hierarchy in these populations. The average amount of competition each tree was subject to was a predictor of the inequality of size at all four sites, and of the inequality of size increment at two of the four sites. However, changes in competition, or at least the way that it was quantified here, was not generally sufficient to explain the observed inter-annual variation in the inequality of size increment. This contention is supported by the fact that the annual growth rate was a significant predictor of inequality in size increment at all four sites. Secondly, there was a high degree of variability in inequality in size increment from year to year, even though the coefficient of variation (CV%) of the competition index showed that each tree was subject to a relatively similar amount of competition in a given year, and that the overall variability in the competition index stayed relatively constant from year to year.

In jack pine, poor growth is likely related to drought or defoliation, the dominant agents of selection on the sandy, nutrient poor sites on which this species is dominant in this region. In most years, inequality in size increment was primarily due to large numbers of trees with low growth rates (Figure 5.2), but was also due to small numbers of trees with high growth rates during some years of low growth rate, at some sites. For example, the period with high values for the Lorenz coefficient of asymmetry for the rich site at Candle Lake during the 1960s (Figure 5.2) was coincident with a period of defoliation (Volney 1988), suggesting that defoliation caused inequality in size increment to be due to a small number of trees with large growth rates. The trees with large growth rates during these years likely escaped defoliation, and would be in a position of relative

competitive advantage. Defoliation in jack pine causes greater mortality in suppressed than dominant trees (Gross 1992), and escaping defoliation may be one of the factors that allowed the surviving trees to become dominant.

Previous studies have shown that competitive status of trees affects their response to variation in precipitation. For example, Wichmann (2001) and Orwig and Abrams (1997) have noted that increased water availability benefits large trees more than small trees. In a study of European beech, Piutti and Cescatti (1997) showed that growth was negatively correlated with precipitation under water deficit conditions for small trees, but that growth in large trees showed no relationship with water deficit conditions. Similarly, Orwig and Abrams (1997) showed that, in general, small trees were more severely affected by drought than large trees for a wide variety of species and site types. In contrast to the periods of defoliation, the general trend in this study was that inequality in size increment was mostly due to a large number of trees with small growth rates (Figure 5.2). These trees that performed poorly may have been poorly adapted to drought, possibly due to inappropriate genetics, poor micro-site or shallow rooting depth. During low precipitation periods, better-adapted trees could maintain some growth and become relatively larger compared to poorly adapted trees during these drought years. Similar to the situation for trees that escape defoliation, this advantage would improve their relative competitive status and allow them to become dominant in future years.

Size was more equal than size increment, and size inequality was also less variable from year to year. In a given region, size inequality was higher at poor than rich sites. This conforms to expectation because self-thinning, which acts to reduce inequality by removing the smallest individuals, typically occurs more slowly at nutrient poor sites. However, this observation may have been confounded by density also being higher at poor sites. The observed greater inequality in size increment also conformed to expectation. In some years, the growth rate for individual trees can be close to zero, which would result in high inequality. In contrast, it is not possible for tree size to be close to zero, so there is less potential for inequality in size. Overall, some combination of stand density, mean tree size and average competition index were significant predictors of size inequality at all sites. These variables all change over time in a highly interactive manner, which was reflected in the variation in the sign and significance of the coefficients for these predictors. The observed relationships were site-specific and not always consistent with the expectation of increasing inequality of size at high stand densities or high levels of competition. Self-thinning mortality generally decreases size inequality by removing the smallest individuals. However, small changes in the relative position of dead trees in the overall size distribution of the stand can result in either increases or decreases in the inequality of the size distribution in the years following a mortality event, and these changes can also be influenced by the growth rate of the surviving trees (Kenkel et al 1997). Factors causing years of high and low growth rate may also concurrently influence the probability of mortality for trees of slightly different size classes. For example, years of high growth rate may increase the probability of mortality for only the smallest trees, as high growth rates may increase the asymmetry of competition and cause "regular" or autogenic mortality associated with stand dynamics (Oliver and Larson 1996). On the other hand, years of low growth rate may increase the probability of mortality for all size classes and cause "irregular" or allogenic mortality

(Oliver and Larson 1996), which is not necessarily exclusively in the smallest size classes, particularly if the causes of low growth are environmental.

Mean tree size, stand density, and average competition were also significant predictors for the inequality of size increment at all but the rich site at Candle Lake, where stand level annual volume increment (lagged by one year) was the only significant predictor. This indicates that inequality in size increment was also somewhat related to variables associated with stand dynamics. Again, however, the sign and significance of the coefficients was not consistent, indicating that observed relationships were also site specific. These inconsistencies are suggestive of changes in the relative importance of one-sided (where small trees have little effect on large trees) and two-sided (where small trees also have an important effect on large trees) competition over time, both of which are observed to occur in even-aged tree populations (Brand and Magnussen 1988). The site-specific nature of the relationships between variables associated with stand dynamics and size and size-increment inequality suggest that the relative importance of these two modes of competition over time is also site-specific.

The results of this study suggest that factors influencing the annual growth rate are also influencing the development of size hierarchy in these forests, and that it is primarily the years with low growth rate that influence this development. Studies quantifying competition effects on tree growth usually measure subject trees and their competitors at a single point in time only, resulting in static estimates of competition indices for only single points in time (Burton 1993). Spatial or aspatial indices of competition (e.g. Lorimer 1983, Tome and Burkhardt 1989, Holmes and Reed 1991, Biging and Dobbertin 1992, Biging and Dobbertin 1995) are the dominant mechanism for generation of size hierarchy in many tree growth models. Using these indices usually result in moderately increased correlations between observed and predicted growth rates over time. However, there is clearly much residual variability in the growth response in these models that is not explained by competition. Schwinning and Weiner (1998) indicated that effect of transient factors like weather variation and defoliation on development of size hierarchies are poorly understood, but the data presented in this study indicate consistent and significant effects of yearly growing conditions. The sensitivity of jack pine to variation in weather (Larsen and MacDonald 1995, Brooks et al 1998, Hofgaard et al 1999) and periodic defoliation by jack pine budworm (Volney 1988, Gross 1992) is clearly important to the differentiation of growth rates of trees within populations since their effects are likely to be different from those induced by density-dependent effects (Thomas and Weiner 1986). Differences in growth rate among trees during years of poor growth may form the basis for development of size hierarchies on which asymmetric competition can act. This suggests that a complete understanding of the process of competition in these forests requires further evaluation of how factors that influence variation in the annual growth rate also affect how size hierarchies are generated in these populations.

5.5 Literature Cited

Biging, G.S., and M. Dobbertin. 1992. A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. For.Sci. 38:695-720.

Biging, G.S., and M. Dobbertin. 1995. Evaluation of competition indices in individual tree growth models. For.Sci. 41:360-377.

Brand, D.G., and S. Magnussen. 1988. Asymmetric, two-sided competion in even aged monocultures of red pine. Can.J.For.Res. 18:901-910.

Brassard, B.W., and H.Y.H. Chen. 2006. Stand structural dynamics of North American boreal forests. Crit.Rev.Plant.Sci. 25:115-137

Brooks, J.R., L.B. Flanagan, and J.R. Ehrlinger. 1998. Responses of boreal conifers to climate fluctuations: indications from tree-ring widths and carbon isotope analyses. Can.J.For.Res. 28:524-533

Burton, P.J. 1993. Some limitations inherent to static indices of plant competition. Can.J.For.Res. 23:2141-2152

Carrer, M., and C. Urbinati. 2001. Spatial analysis of structural and tree-ring related parameters in a timberline forest in the Italian Alps. J.Veg.Sci. 12:643-52

Damgaard, C., and J. Weiner. 2000. Describing inequality in plant size or fecundity. Ecology 81:1139-1142

Dixon, P.M., J. Weiner, T. Mitchell-Olds, and R. Woodley. 1987. Bootstrapping the Gini coefficient of inequality. Ecology 68:1548-1551.

Garcia, O. 2006. Scale and spatial structure effects on tree size distributions: implications for growth and yield modeling. Can.J.For.Res. 36:2983-2993

Gates, D.J., R. McMurtrie, and C.J. Borough. 1983. Skewness reversal of distribution of stem diameter in plantations. Aust.For.Res. 13:267-270.

Gross, H.L. 1992. Impact analysis for a jack pine budworm infestation in Ontario. Can.J.For.Res. 22:818-831.

Halliwell, D.H., and M.J. Apps. 1997. Boreal Ecosystem-Atmosphere Study (BOREAS) biometer and auxiliary sites: overstory and understory data. Nat.Res.Can., Can.For.Serv., North.For.Cent., Edmonton, AB.

Henry, J.D., and J.M.A. Swan. 1974. Reconstructing forest history from live and dead plant material – an approach to the study of forest succession in southwest New Hampshire. Ecology 55:772-783.

Hegyi, F. 1974. A simulation model for managing jack pine stands. pg 74-90 in Fries, J. (ed). Growth models for tree and stand simulation. Royal College of Forestry, Stockholm, Sweden.

Hofgaard, A. J. Tardif, and Y. Bergeron. 1999. Dendroclimatic response of *Picea mariana* and *Pinus banksiana* along a latitudinal gradient in the eastern Canadian boreal forest. Can.J.For.Res. 29:1333-1346.

Hogg, E.H., J.P. Brandt, and B. Kochtubajda. 2005. Factors affecting interannual variation in growth of western Canadian aspen forests during 1951-2000. Can.J.For.Res. 35:610-622.

Hogg, E. H., and R.W. Wein. 2005. Impacts of drought on forest growth and regeneration following fire in southwestern Yukon, Canada. Can.J.For.Res. 35:2141-2150.

Holmes, M.J., and D.D. Reed. 1991. Competition indices for mixed species northern hardwoods. For.Sci. 37:1338-1349

Johnson, E.A., and G.I. Fryer. 1989. Population dynamics in lodgepole pine-engelmann spruce forests. Ecology 70:1335-1345.

Kenkel, N.C., M.L. Hendrie, and I.E. Bella. 1997. A long-term study of *Pinus banksiana* population dynamics. J.Veg.Sci. 8:241-254.

Knox, R.G., R.K. Peet, and N.L. Christensen. 1989. Population dynamics in Loblolly pine stands: changes in skewness and size inequality. Ecology 70:1153-1166.

Larsen, C.P.S., and G.M. MacDonald. 1995. Relations between tree-ring widths, climate, and annual area burned in the boreal forest of Alberta. Can.J.For.Res. 25:1746-1755.

Lorimer, C.G. 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. For.Ecol.Man. 6:343-360

Mohler, C.L., P.L. Marks, and D.G. Sprugel. 1978. Stand structure and allometry of trees during self-thinning of pure stands. Ecology 66:599-614.

Newton. P.F., and V.G. Smith. 1988. Diameter distributional trends within mixed black spruce/balsam fir and pure black spruce stand types. For.Ecol.Man. 25:123-138.

Oliver, C.D., and E.P. Stephens. 1978. Reconstruction of a mixed-species forest in Central New England. Ecology 58:562-572.

Oliver C.D., and B.C. Larson. 1996. Forest Stand Dynamics, Update Edition. John Wiley and Sons, New York, NY.

Orwig, D.A., and M.A. Abrams. 1997. Variation in radio growth responses to drought among species, site, and canopy strata. Trees Struct. Func. 11:474-484.

Pinheiro, J., D. Bates, S. Debroy, and D. Sarkar. 2007. NLME: Linear and Nonlinear Mixed Effects Models. R package version 3.1-81.

Piutti, E, and A. Cescatti. 1997. A quantitative analysis of the interactions between climatic response and intraspecific competition in European beech. Can.J.For.Res. 27:277-284

Ramseier, D., and J. Weiner. 2006. Competitive effect is a linear function of neighbour biomass in experimental populations of *Kochia scoparia*. J.Ecol. 94: 305-309.

R Development Core Team. 2007. R: A Language and Environment for Statistical Computing. R foundation for statistical computing, Vienna.

Schwinning, S, and J. Weiner. 1998. Mechanisms determining the degree of size symmetry in competition among plants. Oecologia 113:447-455

Stoll P., J. Weiner, and B. Schmid. 1994. Growth variation in a naturally established population of *Pinus sylvestris*. Ecology 75:660-670.

Tome, M., and H. Burkhardt. 1989. Distance-dependent competition measures for predicting growth of individual trees. For.Sci. 35:816-831.

Volney, W.J.A. 1988. Analysis of historic jack pine budworm outbreaks in the Prairie provinces of Canada. Can.J. For. Res. 18:1152-1158

Weiner, J. 1990. Asymmetric competition in plant populations. Trends.Ecol.Evol. 5:360-364.

Weiner, J. 1995. Follwing the growth of individuals in crowded plant populations. Trends.Ecol.Evol. 10:389-390.

Weiner, J., and O.T. Solbrig. 1984. The meaning and measurement of size hierarchies in plant populations. Oecologia 61:334-336.

Weiner, J., and S.C. Thomas. 1986. Size variability and competition in plant monocultures. Oikos 47:211-222.

Weiner, J., and C. Damgaard. 2006. Size-asymmetric competition and size-asymmetric growth in a spatially explicit zone-of-influences mode of plant competition. Ecol.Res. 21:770-712.

Westoby, M. 1982. Frequency distributions of plant size during competitive growth of stands: the operation of distribution modifying functions. Ann.Bot. 50:733-735.

Wichmann, L. 2001. Annual variations in competition symmetry in even-aged sitka spruce. Ann.Bot. 88:145-151

Table 5.1. Parameter estimates, standard errors and p-values for the regression model for inequality of size and size increment. Parameters in bold were significant at $\alpha<0.05$. The variables are in the table are stand density (DENS), mean tree volume (SIZE), average amount of competition each tree is subject to (COMP), where competition is calculated using a distance weighted absolute size index, and stand level annual volume increment in the current year (AVI), and one year previously (AVI1).

	Candle Lake – Rich			Candle Lake – Poor			Thompson – Rich			Thompson – Poor		
	β	SE β	p	β	SE β	p	β	SE β	p	β	SE β	p
Volume												
Intercept	**2.3×10^{-1}**	**4.6×10^{-2}**	**<0.01**	**1.6×10^{-1}**	**1.1×10^{-2}**	**<0.01**	**2.1×10^{-1}**	**2.8×10^{-2}**	**<0.01**	**5.5×10^{-1}**	**8.8×10^{-3}**	**<0.01**
DENS	**1.5×10^{-4}**	**1.8×10^{-5}**	**<0.01**	**1.1×10^{-4}**	**4.0×10^{-6}**	**<0.01**	**9.7×10^{-5}**	**1.6×10^{-5}**	**<0.01**	**-2.1×10^{-5}**	**2.3×10^{-6}**	**<0.01**
SIZE	**3.9×10^{-1}**	**1.2×10^{-1}**	**<0.01**	**1.1×10^{0}**	**9.9×10^{-2}**	**<0.01**	1.6×10^{-1}	1.4×10^{-1}	0.26	**-1.2×10^{0}**	**2.6×10^{-1}**	**<0.01**
COMP	**-3.2×10^{-3}**	**3.7×10^{-4}**	**<0.01**	**-1.0×10^{-3}**	**1.0×10^{-4}**	**<0.01**	**-8.1×10^{-4}**	**1.3×10^{-4}**	**<0.01**	**-1.4×10^{-3}**	**1.0×10^{-4}**	**<0.01**
AVI	7.2×10^{-4}	1.4×10^{-3}	0.61	3.8×10^{-4}	9.9×10^{-4}	0.70	9.5×10^{-4}	1.1×10^{-3}	0.41	-2.4x10-3	2.7x10-3	0.37
AVI1	**4.4×10^{-3}**	**1.4×10^{-3}**	**<0.01**	-1.0×10^{-3}	9.9×10^{-4}	0.32	-1.3×10^{-3}	1.0×10^{-3}	0.22	-3.9x10-3	2.8x10-3	0.17
Adjusted R^2		**0.97**	**<0.01**		**0.99**	**<0.01**		**0.98**	**<0.01**		**0.85**	**<0.01**
Volume Increment												
Intercept	3.1×10^{-1}	2.5×10^{-1}	0.23	**4.1×10^{-1}**	**8.9×10^{-2}**	**<0.01**	**6.4×10^{-1}**	**2.0×10^{-1}**	**<0.01**	**8.2×10^{-2}**	**5.7×10^{-2}**	**<0.01**
DENS	1.3×10^{-4}	9.7×10^{-5}	0.18	-2.5×10^{-5}	3.1×10^{-5}	0.42	-1.4×10^{-5}	1.1×10^{-4}	0.89	**-1.2×10^{-4}**	**1.5×10^{-5}**	**<0.01**
SIZE	1.0×10^{0}	6.6×10^{-1}	0.12	-1.2×10^{0}	7.7×10^{-1}	0.12	-4.7×10^{-1}	9.9×10^{-1}	0.63	**-1.1×10^{1}**	**1.7×10^{0}**	**<0.01**
COMP	-1.9×10^{-3}	1.9×10^{-3}	0.32	**3.7×10^{-3}**	**8.2×10^{-4}**	**<0.01**	-1.0×10^{-3}	9.6×10^{-4}	0.28	**6.1×10^{-3}**	**6.5×10^{-4}**	**<0.01**
AVI	-2.8×10^{-3}	7.6×10^{-3}	0.71	-1.4×10^{-2}	7.8×10^{-3}	0.07	**-2.0×10^{-2}**	**8.2×10^{-3}**	**0.02**	**-4.9×10^{-2}**	**1.7×10^{-2}**	**<0.01**
AVI1	**-2.4×10^{-2}**	**7.5×10^{-3}**	**<0.01**	**-2.0×10^{-2}**	**7.8×10^{-3}**	**0.01**	-8.8×10^{-3}	7.2×10^{-3}	0.23	-1.9×10^{-2}	1.8×10^{-2}	0.29
Adjusted R^2		**0.41**	**<0.01**		**0.54**	**<0.01**		**0.42**	**<0.01**		**0.85**	**<0.01**

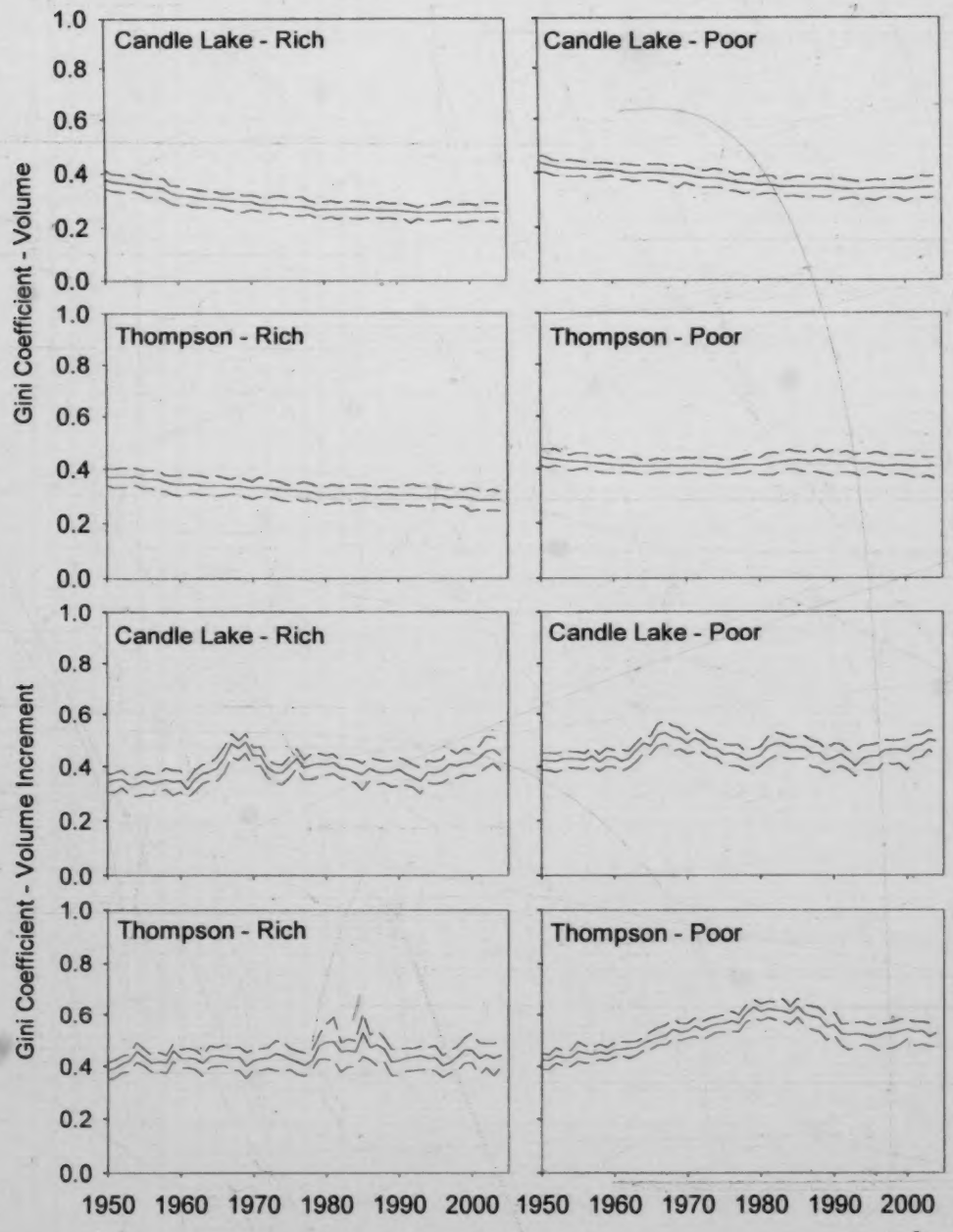

Figure 5.1. Annual trajectories of the Gini coefficient for cumulative volume and volume increment since 1950 at each 900 m^2 study plot. The solid line represents the Gini coefficient, the dashed lines are 95% confidence intervals calculated from 1000 bootstrap samples.

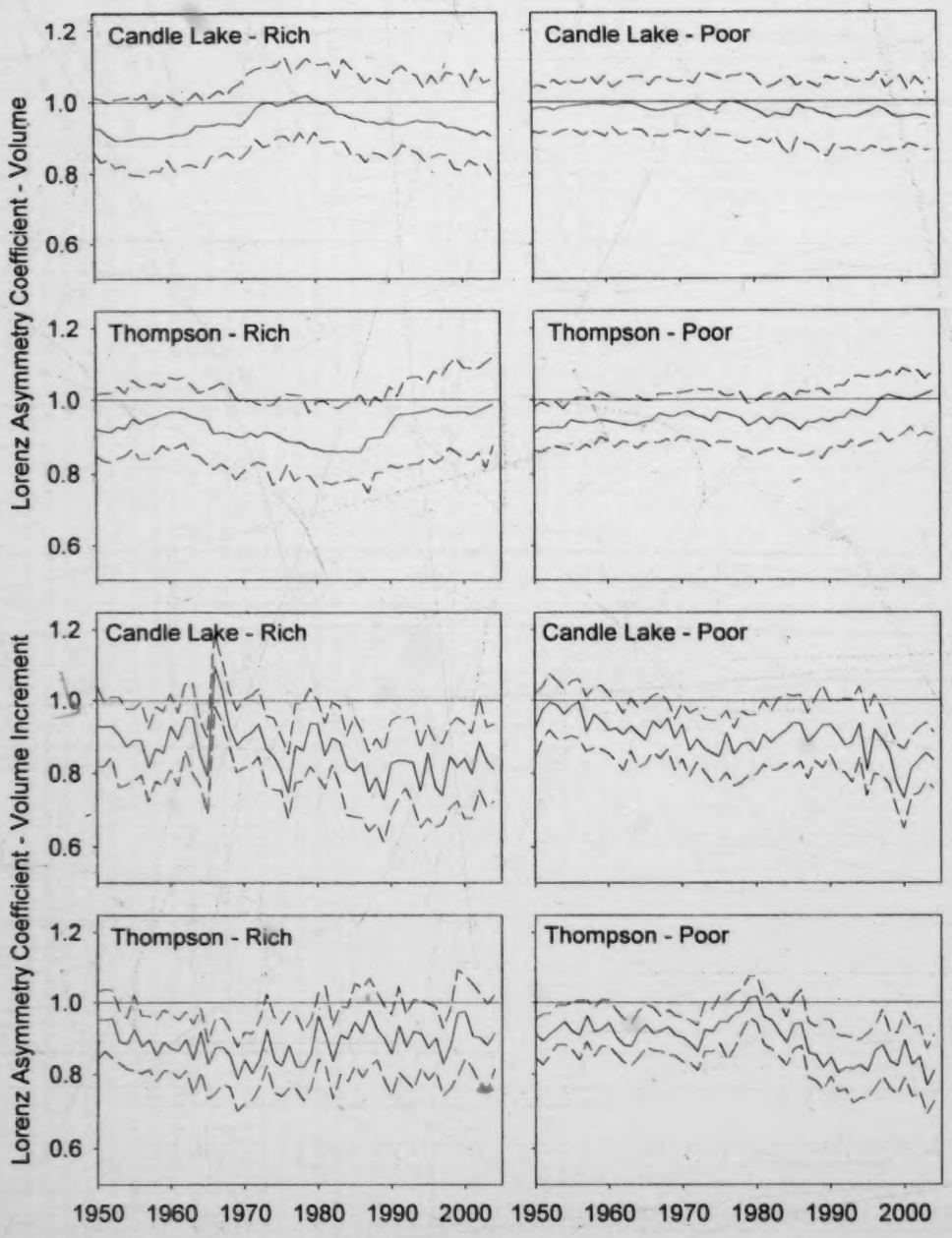

Figure 5.2. Annual trajectories of the Lorenz asymmetry coefficient for cumulative volume and volume increment since 1950 at each 900 m^2 study plot. The straight line indicates the value one, where the Lorenz curve is symmetric. The solid line represents the Lorenz asymmetry coefficient, the dashed lines are 95% confidence intervals calculated from 1000 bootstrap samples

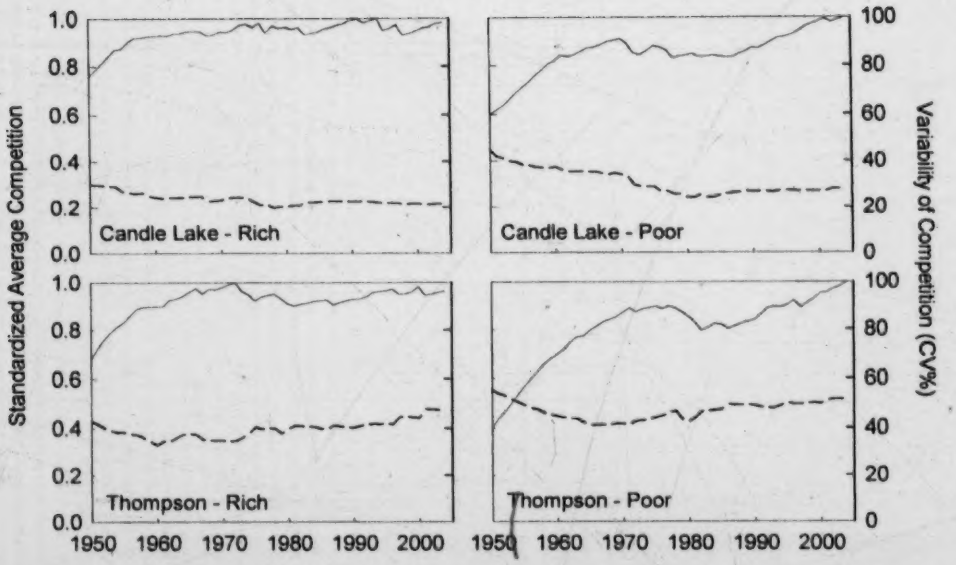

Figure 5.3. Annual trajectories of the average amount of competition each tree is subject to (solid line) and the coefficient variation (CV%) of competition each tree is subject to (dashed line) at each study plot. Competition was quantified using a distance-weighted absolute size index (Eq 5.1), with a variable search radius defined as 3.5x each tree's crown width.

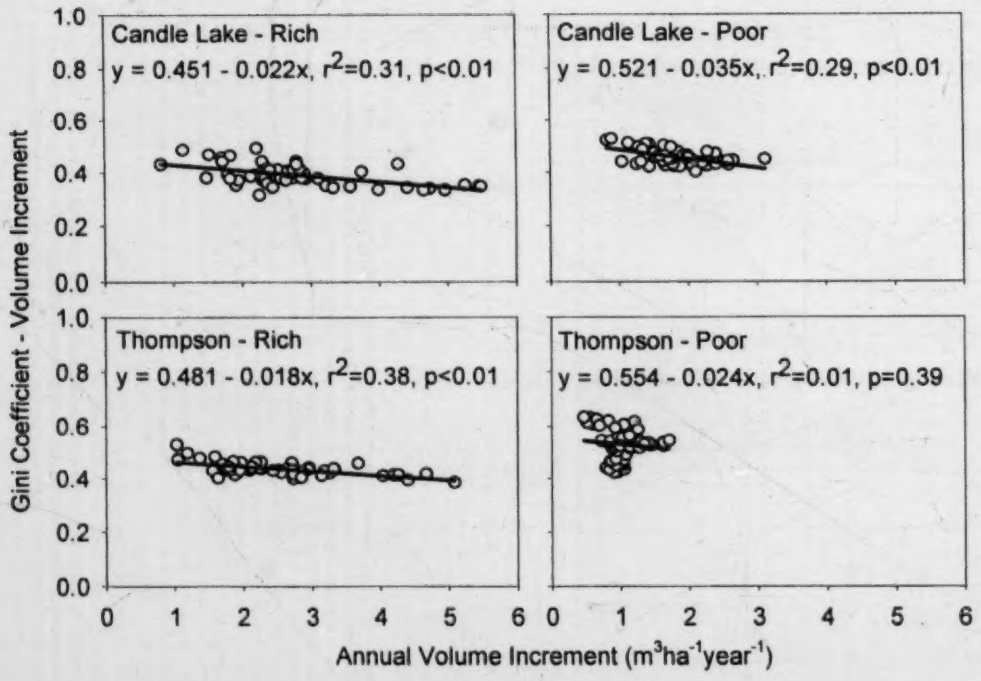

Figure 5.4. Relationship between the inequality of annual volume increment, as quantified by the Gini coefficient, and annual volume increment

6.0 Magnitude and causes of annual variation in the mode of competition in *Pinus banksiana*

In tree populations, the mode of competition for resources that can be depleted (e.g. nutrients, water) is symmetric (two-sided). Individual trees obtain these resources in proportion to their size. The mode of competition for resources that can be pre-empted (e.g. light) is asymmetric (one-sided). Larger (taller) trees obtain a disproportionate amount of these resources than expected based upon their size alone (Weiner and Thomas 1986, Weiner 1990, Schwinning and Weiner 1998). Stand development theories predict that a size hierarchy develops at the onset of stem exclusion, followed by self-thinning that causes mortality primarily by a process of asymmetric competition, as larger individuals gradually pre-empt light by shading smaller individuals (Oliver and Larson 1996). The results of this process can generally be predicted by changes in the size, density, and area of influence of trees over time. As a result, most models of forest stand development assume that asymmetric competition, where large individuals out-compete smaller neighbours, is the dominant process influencing the development of stands. However, competition in even-aged single species stands inherently consists of both symmetric and asymmetric components (Brand and Magnussen 1988). The importance of these modes of competition may vary over time, in response to transient fluctuation in growing conditions caused by factors like variation in precipitation or insect attack that may affect larger trees differently than smaller trees. It is not well understood how these fluctuations in growing condition might affect stand development (Schwinning and Weiner 1998).

Some studies show that increased water availability benefits dominant trees (Orwig and Abrams 1997, Wichmann 2001) and negatively influences suppressed trees (Vose and Swank 1994). In contrast, others show that suppressed trees suffer less growth loss under drought (Liu and Muller 1993), and grow relatively better (Piutti and Cescatti 1997). Under severe water deficits, competition may in fact become negatively asymmetric, where small trees obtain disproportionately more resources than large trees (Biondi 1996). The mechanism generating negative asymmetric competition during water deficit may be the ability for smaller plants to keep stomates open longer because of the lower evaporative demand of their mid canopy position (Barnes et al 1990, Liu and Muller 1993). Further studies show that reactions to drought occur in a species and site specific manner (Abrams and Mostoller 1995, Orwig and Abrams 1997). The relative sensitivity of trees of different size classes to environmental variability may vary even within the same species. Small Norway spruce (*Picea abies* L.) trees may either be more (van der Brakel and Visser 1996) or less (Makinen et al 2002) sensitive to environmental variability than large trees. In general, the reaction of trees of different size classes to water availability is not well understood.

The influence of defoliation on trees of different size classes is also requires further study. Conceptually, if larger trees were disproportionately defoliated, smaller individuals would continue to grow, reducing size hierarchy, resulting in more symmetric competition. Conversely, a disproportionate defoliation of smaller trees would increase size hierarchy, resulting in more asymmetric competition. Previous studies suggest that

the main effect of defoliation is to increase the asymmetry of competition by delaying the recovery of small trees (Newton and Joliffe 1998) or by increasing their probability of mortality (Gross 1992). These results suggest that defoliation may act as a catalyst that switches stands between different competitive states. For example, a defoliation my incite the development of a size hierarchy, upon which asymmetric competition can then act to further differentiate trees into crown classes. In the absence of this growth variation, it is possible that this differentiation would not occur, resulting in stagnation (Oliver and Larson 1996). However, the results of a specific defoliation event are likely dependent upon the stage of stand development at which the defoliation occurs, and the size proportionality of its effects. These effects are difficult to predict because the effect of defoliation on an individual tree is a complex function of the number and relative palatability of its neighbors (Augner et al 1997).

Investigating changes in the mode of competition over time in tree populations is challenging because it is difficult to obtain the detailed, long-term annual data on size, growth rate, and mortality that are required. Here, I was able to obtain such data using tree-ring reconstruction. Jack pine growth has been related to inter-annual variation in weather (Larsen and MacDonald 1995, Brooks et al 1998, Hofgaard et al 1999). In this region, they are also subject to defoliation by jack pine budworm (*Choristoneura pinus pinus* Freeman) on about a ten year cycle (Volney 1988). These defoliation events often result in a mixture of defoliated and non-defoliated trees (Scarr 1995). The complex nature of the interactions between site factors, defoliation, pollen cone production, and susceptibility to root disease (Mallett and Volney 1990, McCollough 2000, Nealis et al 2003) make the impact of defoliation on jack pine stand development difficult to predict. I hypothesized that weather and defoliation are the primary factors influencing annual variation in the mode of competition in jack pine forests in this region. I also hypothesized that inter-annual variation in stand level growth rate might be a good proxy variable for prediction of mode of competition as stand growth rate accounts for all the environmental factors influencing a stand. I have previously shown in chapter 5 that differential growth of individuals during years with low growth rates strongly influences the development of size hierarchies. The objectives of this chapter were to determine the magnitude and causes of inter-annual variability in the mode of competition at a range of jack pine stands of different climatic, disturbance, and nutritional status. I also tested which factors (defoliation, weather variation, or growth rate) are the best predictors of annual changes in the mode of competition.

6.1 Methods

6.1.1 Field and laboratory

Field data collection and laboratory sample processing were conducted as described in chapter 1. Cumulative ring-widths for a given tree *i* in year *j* were converted to volume (V_{ij}) and were also summed to get total standing volume in year *j* ($Vtot_j$). Similarly, ring-widths in a given year *i* in year *j* were converted to annual volume increment (AVI_{ij}), and total annual volume increment in year *j* ($AVItot_j$). These methods are described in chapter 2 and again in chapter 4. In this chapter, I use data from both the

900 m^2 plots at Thompson and Candle Lake, and the 100 m^2 plots at Prince Albert, Flin Flon, and Jenpeg because the analyses here do not require spatial data.

6.1.2 Mode of competition

Changes in the mode of competition were assessed by an index of competitive symmetry that was calculated annually at each stand. This index quantifies the relative proportionality between growth rate and tree size in a population, and is based on the distribution modifying concept (Westoby 1982, Weiner 1990, Wichmann 2001, Weiner and Damgaard 2006). It is analogous to indices described in Schwinning and Weiner (1988) and Nord-Larsen et al (2006), and to indices used in forage preference studies for wildlife (e.g. Månsson et al 2007). To calculate this index, the proportion of total stand volume ($V_{ij}/Vtot_j$) that each tree represented in a given year *Y* was plotted against the proportion of total stand volume growth ($AVI_{ij}/AVItot_j$) that each tree represented in year *Y+1*. The index is the slope of the linear regression line fit to these data. A centered log ratio transformation (Aitchison 1986) was applied to each prior to fitting a linear regression line. If there are *d* trees in a given year, and p_i is the proportion of total size or size increment (i = 1,2,..,d) in each tree in that year, then the centered log-ratio transformation is calculated as

$$\log(p_i/g) \qquad (4)$$

where $g = (p_1,p_2,..,p_d)^{1/d}$, or the geometric mean of all the proportional tree sizes or size increments in a given year (Aitchison 1986). When the growth of trees is proportional to their size, competition is symmetric, and the slope of the best fitting regression line should be 1. When growth in large trees is disproportionately high relative to their size, the slope of this line is greater than 1 and competition is positively asymmetric. When growth in small trees is disproportional high, the slope is less than 1 and competition is negatively asymmetric (Figure 6.1). In Figure 6.2, I demonstrate how the relationship between growth rate and size used in the calculation of the index of competitive symmetry for a set of example data at 10 year intervals from the poor site at Thompson.

6.1.3 Climate data

I obtained spatially interpolated data on the mean monthly minimum and maximum temperatures and total monthly precipitation from 1950 to 1999 for each site from the database described by McKenney et al (2006). After 2000, I obtained these from the nearest weather station in the Meteorological Service of Canada's online data repository (http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_e.html). Growth rate of jack pine is positively correlated with spring temperatures (Brooks et al 1998, Hofgaard et al 1999), precipitation in the current year, and precipitation in the previous year (Larsen and MacDonald 1995, Brooks et al 1998). As a result, I tested the following as predictors of annual changes in the mode of competition: mean April temperature in the current year (APRIL), total growing season precipitation in the current year (PREC), and total growing season precipitation in the previous year (PREC1). I also calculated a climate moisture index using the method described in Hogg (1997) to test if a composite variable accounting for both temperature and precipitation would be a better

predictor. This was calculated for both the current (CMI) and previous (CMI1) growing season.

6.1.4 Insect defoliation data

I determined likely years of past insect outbreaks for each site from (1) the tables in Simpson and Coy (1999), (2) indices of jack pine budworm severity in Volney (1988), and (3) by interpreting the historical annual reports of the Canadian Forest Insect and Disease Survey. I cross-referenced these reports of defoliation with the tree-ring data to confirm that defoliation actually occurred during those years. Based on these data sources, I determined that the likely years of defoliation were 1964-66 1976-78, and 1984-87 at the Prince Albert sites 1964-67 1978, and 1985-87 at the Candle Lake sites 1965-67 and 1984-86 at the Flin Flon sites 1984-85 at the Jenpeg sites, and 1983-85 at the Thompson sites. There were no data on the severity of defoliation during these years that was specific for the study plots, so these were simplified to an index of defoliation for years when it occurred (1), and years when it did not (0).

6.1.5 Annual variation in stand level growth rate

I hypothesized that stand level annual volume increment may also influence inter-annual variation in competition symmetry because it is a proxy variable that accounts for all the potential environmental factors influencing growing conditions. I scaled data from ring-widths at breast height to tree level volume increment using the methods described in chapter 2 and again in chapter 4. I summed the individual tree volume increments in a given year to determine annual stand level annual volume increment at each site.

6.1.6 Data analysis

I used an information-theoretic approach to rank thirteen models (Table 6.1) in terms of their ability to explain annual changes in the competitive symmetry index. Each model embodies a different hypothesis about the factors that I proposed to affect variation in growing conditions, and therefore influence the mode of competition (see Introduction). In chapter 5, I have shown that the inequality of volume and volume increment are both related to variables associated with stand development, so I included stand age (AGE) and stand density (DENS) in each proposed model. I assumed that further residual variability in the mode of competition would be due to either (1) the weather variables observed in previous studies to be correlated with jack pine growth, (2) periodic defoliation by jack pine budworm, or (3) stand level annual volume increment. Akaike's Information Criterion (AIC) was used to rank models based on their ability to explain the data, and Akaike weights (w) to estimate the relative likelihood of each model in Table 6.1, given the data (Burnham and Anderson 2002). The Akaike ratio is calculated as the ratio of the largest Akaike weight (w_{max}) relative to the Akaike weight of a given model (w_i). Models with an Akaike ratio less than 2 were considered to be reasonably supported. Each model was fit using the GLS function in the NLME package (Pinheiro et al 2007) for R (R Development Core Team 2007). Residuals were assumed to follow a first order autoregressive (AR1) error structure, and the parameters were estimated by maximizing the log-likelihood. For the model that generally received the most empirical support when all sites were considered together, I also further examined the regression coefficients for the predictor variables of that model.

6.2 Results

The index of competitive symmetry increased over time at most sites (Figure 6.3). However, there was also variability in the trajectories, both within and among sites. At all sites, there were also periods of time when competition was symmetric. At some sites, the symmetry of competition stayed relatively constant for long periods of time, while others showed large, sudden fluctuations, occasionally resulting in periods of negative asymmetric competition. Due to their smaller sample size, the 100 m^2 plots exhibited fluctuations of a greater magnitude than the 900 m^2 plots. Otherwise, there were neither apparent differences in the magnitude or trends between rich and poor sites, nor any clear geographic effects.

Competitive symmetry was strongly related to annual growth rate at 8 out of 10 sites. The most probable model at six sites was model 2, where annual changes in the index of competitive symmetry were predicted as a function of stand age, density, and annual growth rate in the current year (Table 6.2). At two sites, model 3, which also included annual growth rate lagged by one year, was the most probable model. The exceptions to this trend were at the rich site at Prince Albert and the rich site at Flin Flon. Age and density alone (model 1) were sufficient to explain changes in the strength of competition at the rich site at Prince Albert. No model sufficiently explained changes in competition at the rich site at Flin Flon. Several had AIC ratios less than 2 and all had a poor goodness of fit.

Overall, model 2 received the most empirical support. The regression coefficients (β) for the stand dynamics variables, age and density, were both positive for model 2 (Table 6.3). This indicates that during periods of constant density in a given stand, competitive asymmetry increases with age (time), and that at a given age (time), competition will be most asymmetric at the highest density stands. This is consistent with previous studies of where mortality is controlled to some threshold level (e.g. Weiner and Thomas 1986 and references therein). After stand development was taken into account, annual volume increment is a significant predictor of changes in the index of competition symmetry at all sites except the rich sites at Prince Albert and Flin Flon, where this model received the least empirical support (Table 6.3). At the sites were annual volume increment was a significant predictor, the sign of the regression coefficient was positive, indicating that as growth rate increased, competition symmetry also increased, and when growth rate decreased, competition symmetry also decreased. This relationship is demonstrated graphically in Figure 6.4.

6.3 Discussion

In this chapter, I used tree-ring data to reconstruct the mode of competition 50 years into the past at ten jack pine stands. The strength of asymmetric competition was related to stand age and density, and also to stand-level growth rate. During periods when growth increased from one year to the next, competition became more asymmetric. This is presumably due to sufficient soil moisture and therefore greater importance of competition for light. When growth decreased from one year to the next, competition became more symmetric. This suggests that factors reducing growth also reduced the

importance of competition for light and increased the importance of competition for soil resources. In chapter 5, I showed that variation in growth rate is also an important factor influencing the development of size hierarchies, indicating that variation in growth rate has several important impacts on the dynamics of forest stands.

The observed degree of inter-annual variability in stand level growth rate suggests that growing conditions did in fact vary. Under the assumption that stand-level growth rate is a good proxy for growing conditions, these results indicate that there is a relationship between the mode of competition and growing conditions. However, the weather and defoliation variables that I hypothesized to cause growing conditions to vary were not good predictors of changes in the mode of competition. This may be due to several reasons. First, the relationships between growth and climate in jack pine, while statistically significant, usually have low explanatory power (Larsen and MacDonald 1995, Brooks et al 1998, Hofgaard et al 1999). Second, weather data that I used may not have accurately reflected conditions at my study sites. In particular, localized variation in precipitation is difficult to interpolate (McKenney et al 2006, Wang et al 2006). Third, the factors causing variation in growing conditions for jack pine may be specific to a given region. For example, Hogg et al (2005) show that growth in trembling aspen in western Canada is related more strongly to water availability than insect defoliation, while Cooke and Roland (2007) showed the opposite relationship for trembling aspen in central Canada. Jack pine exhibit strong clinal variation (van Niejenhuis and Parker 1996), suggesting a possible genetic basis for site-specific climate adaptations, so it may not have been possible to detect effects from a single set of climate predictor variables. The effects of variation in weather on the mode of competition will require a site-specific assessment of the climatic factors influencing growth at a specific site.

I also hypothesized that, in some cases, defoliation may act as a catalyst that switches stands between competitive states. Though I was unable to link periods of defoliation specifically with changes in competition symmetry, there were some defoliation events which seemed to be coincident with a change in the overall trend in competitive symmetry. Newton and Jolliffe (1988) suggested that defoliation in density stressed black spruce shifted stands from a state of size-asymmetric competition to a state of asymmetric competition because the growth of large trees recovered more quickly. Inspection of Figure 6.3 shows that defoliation in the 1980's coincides with an increase in the index of competitive symmetry at the rich site at Prince Albert, but this was not a universal pattern. Defoliation events in the mid 1980's coincide with the onset of a decline in the index of competitive symmetry at the rich site at Flin Flon, the poor site at Jenpeg, and the rich site at Thompson. Small fluctuations in the index of competition symmetry also coincide with defoliation at several sites, but these are not associated with in any persistent changes in the trend. Other cases show no apparent effect.

Early instars of jack pine budworm feed primarily on pollen cones (McCollough 2000 and references therein) and stress-induced crops of pollen cones have been observed on small trees, or trees affected by root rot (Malley and Volney 1990). Feeding primarily on small trees would have a disproportionate effect on these individuals, making competition more asymmetric. As in other studies (Gross 1992), I did see this at some sites. I also showed that competition sometimes became more symmetric after

defoliation, suggesting a disproportionate impact on large trees. This could occur if larger trees produced disproportionately more pollen cones, particularly if defoliation increased their susceptibility to further growth reduction by root rot (Mallett and Volney 1990). In chapter 5, I found that the inequality in growth rate during some defoliation events was mainly due to small numbers of trees that maintain high growth rates. The results here suggest that it was sometimes the larger trees and sometimes the smaller trees that maintained high growth rates during defoliation. This variability may be related to variability in the size proportionality of reproductive output in the population. Reproductive output is often correlated with plant size. In jack pine, most trees produce pollen cones in most years and in the absence of defoliation, total cone production is correlated with growing conditions (Houle and Filion 1993, Despland and Houle 1997). Cone production is often reduced after defoliation (Nealis et al 1997). However, the size proportionality of pollen cone production has not been studied.

In this chapter, I showed that when growing conditions are poor and growth rates go down from one year to the next, the rate at which smaller individuals become further suppressed by large individuals is reduced. In some cases, small individuals may even regain some competitive status if the point of negative asymmetry is reached. Relatively better growth of smaller trees during poor growth may be due to increased ability for compensatory root growth (Brisson and Reynolds 1997), shelter from excessive radiation and water loss during drought (Barnes et al 1990, Liu and Muller 1993), or avoidance by defoliators (Scarr 1995, Augner et al 1997). These results have implications for the design of the indices that are often used to quantify the effect of competition and drive the development of size hierarchies in forest growth and stand dynamics models (e.g. Lorimer 1983, Tome and Burkhardt 1989, Holmes and Reed 1991, Biging and Dobbertin 1992, Biging and Dobbertin 1995). The limitations of these indices, particularly when they are based only single measurements, have previously been discussed (Burton 1993). These indices assign a constant growth advantage to larger trees, which is true when growing conditions are good and growth increases from the previous year. It is not necessarily true when growing conditions are poor and growth decreases from the previous year. This possibility is not presently accounted for by these models.

6.4 Literature Cited

Abrams, M.D., and S.A. Mostoller. 1995. Gas exchange, leaf structure, and nitrogen in contrasting successional tree species growing in open and understory sites during a drought. Tree Physiology 15:361-370.

Aitchison, J. 1986. The statistical analysis of compositional data. Chapman and Hall, London, UK.

Augner, M., J. Tuomi, and M. Rousi. 1997. Effects of defoliation on competitive interactions in European white birch. Ecology 78:2369-2377.

Barnes, P.W., W. Beyschlag, R. Ryel., S.D. Flint, and M.M. Caldwell. 1990. Plant competition for light analyzed with a multispecies canopy model. III. Influence of canopy structure in mixtures and monocultures of wheat and wild oat. Oecologia 82:560-566.

Biging, G.S., and M. Dobbertin. 1992. A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. For.Sci. 38:695-720.

Biging, G.S., and M. Dobbertin. 1995. Evaluation of competiton indices in individual tree growth models. For.Sci. 41:360-377.

Biondi, F. 1996. Decadal-scale dynamics at the Gus Pearson Natural Area: evidence for inverse (a)symmetric competition? Can.J.For.Res. 26: 1397-1406.

Brand, D.G., and S. Magnussen. 1988. Asymmetric, two-sided competion in even aged monocultures of red pine. Can.J.For.Res. 18:901-910.

Brooks, J.R., L.B. Flanagan, and J.R. Ehrlinger. 1998. Responses of boreal conifers to climate fluctuations: indications from tree-ring widths and carbon isotope analyses. Can.J.For.Res. 28:524-533

Brisson, J., and J.F. Reynolds. 1997. Effects of compensatory growth on population processes: a simulation study. Ecology 78:2378-2384.

Burnham, K. P., and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd Edition. Springer-Verlag, New York.

Burton, P.J. 1993. Some limitations inherent to static indices of plant competition. Can.J.For.Res. 23:2141-2152

Cooke, B.J., and J. Roland. 2007. Trembling aspen responses to drought and defoliation by forest tent caterpillar and reconstruction of recent outbreaks in Ontario. Can.J.For.Res. 37:1586-1598.

Despland, E., and G. Houle. 1997 Climate influences on growth and reproduction of *Pinus banksiana* (Pinaceae) at the limit of the species distribution in eastern North America. Am.J.Bot 84:928-937.

Gross, H.L. 1992. Impact analysis for a jack pine budworm infestation in Ontario. Can.J.For.Res. 22:818-831.

Hofgaard, A. J. Tardif, and Y. Bergeron. 1999. Dendroclimatic response of *Picea mariana* and *Pinus banksiana* along a latitudinal gradient in the eastern Canadian boreal forest. Can.J.For.Res. 29:1333-1346.

Hogg, E.H. 1997. Temporal scaling of moisture and the forest-grassland boundary in western Canada. Ag.For.Met. 84:115-122.

Hogg, E.H., J.P. Brandt, and B. Kochtubajda. 2005. Factors affecting interannual variation in growth of western Canadian aspen forests during 1951-2000. Can.J.For.Res. 35:610-622.

Holmes, M.J., and D.D. Reed. 1991. Competition indices for mixed species northern hardwoods. For.Sci. 37:1338-1349.

Houle, G., and F. Filion. 1993. Interannual variations in the seed production of *Pinus banksiana* at the limit of the species distribution in northern Quebec, Canada. Am.J.Bot. 80:1242-1250.

Larsen, C.P.S., and G.M. MacDonald. 1995. Relations between tree-ring widths, climate, and annual area burned in the boreal forest of Alberta. Can.J.For.Res. 25:1746-1755.

Liu, Y., and R.N. Muller. 1993. Effect of drought and frost on radial growth of overstorey and understorey stems in a deciduous forest. Am.Mid.Nat. 129:19-25.

Lorimer, C.G. 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. For.Ecol.Man. 6:343-360

Mäkinen, H., P. Nöjd, and A. Isomäki. 2002. Radial, height, and volume increment in *Picea abies* (L.) Karst stands with varying thinning intensities. Scand.J.For.Res.17: 304-316.

Mallett, K.I., and W.J.A. Volney. 1990. Relationships among jack pine budworm damage, selected tree characteristics, and Armillaria root rot in jack pine. Can.J.For.Res. 20:1791-1795.

McCullough, D.G. 2000. A review of factors affecting the population dynamics of jack pine budworm (*Choristoneura pinus pinus* Freeman). Pop.Ecol. 42:243-256.

McKenney, D.W., J.H. Pedlar, P. Papadol, and M.F. Hutchinson. 2006. The development of 1901–2000 historical monthly climate models for Canada and the United States. Ag.For.Met. 138:69-81

Månsson, J., H. Andrén, H., Å. Pehrson, and R. Bergström. 2007. Moose browsing and forage availability, a scale dependent relationship? Can. J. Zool. 85: 372-380.

Nealis, V.G., S. Magnussen, and A.A. Hopkin. 2003. A lagged, density-dependent relationship between jack pine budworm *Choristoneuara pinus pinus* and its host *Pinus banksiana*. Ecol.Entomology 28:183-192.

Newton, P.F., and P.A. Jolliffe. 1998. Temporal size-dependent growth processes within density-stressed black spruce stands: competition processes and budworm effects. For.Ecol.Man. 111:1-13.

Nord-Larsen, T., C. Damgaard, and J. Weiner. 2006. Quantifying size-asymmetric growth among individual beech trees. Can.J.For.Res. 36:418-425

Oliver C.D., and B.C. Larson. 1996. Forest Stand Dynamics, Update Edition. John Wiley and Sons, New York, NY.

Orwig, D.A., and M.A. Abrams. 1997. Variation in radial growth responses to drought among species, site, and canopy strata. Trees Struct. Func. 11:474-484.

Pinheiro, J., D. Bates, S. Debroy, and D. Sarkar. 2007. NLME: Linear and Nonlinear Mixed Effects Models. R package version 3.1-81.

Piutti, E, and A. Cescatti. 1997. A quantitative analysis of the interactions between climatic response and intraspecific competition in European beech. Can.J.For.Res. 27:277-284

R Development Core Team. 2007. R: A Language and Environment for Statistical Computing. R foundation for statistical computing, Vienna.

Scarr, T. 1995. Phenotypic variation in jack pine susceptibility to jack pine budworm. *In*: Volney, W.JA., V.G. Nealis, G.M. Howse, A.R. Westwood, D.G. McCullough, and B.L. Laishley (eds). Jack pine budworm biology and management. Proceedings of the jack pine budworm symposium, January 24-26, 1995, Winnipeg, MB. Can.For.Serv. Northwest Reg. Inf. Rep. NOR-X-342, Edmonton, AB, pp 79-88.

Schwinning, S, and J. Weiner. 1998. Mechanisms determining the degree of size symmetry in competition among plants. Oecologia 113:447-455

Simpson, R., and D. Coy. 1999. An ecological atlas of forest insect defoliation in Canada 1980-1996. Nat.Res.Can., Can.For.Serv., Atl.For.Cent., Fredericton, NB. Inf.Rep. M-X-206E.

Tome, M., and H.E. Burkhardt. 1989. Distance-dependent competition measures for predicting growth of individual trees. For.Sci. 35:816-831.

van den Brakel, J.A., and H. Visser. 1996. The influence of environmental conditions on tree-ring series of Norway spruce for different canopy and vitality classes. For.Sci. 42:206-219.

van Niejenhuis, A., and W.H. Parker. 1996. Adaptive variation in jack pine from north central Ontario as determined by short-term common garden tests. Can.J.For.Res. 26:2006-2014

Volney, W.J.A. 1988. Analysis of historic jack pine budworm outbreaks in the Prairie provinces of Canada. Can.J.For.Res. 18:1152-1158

Vose, J.M., and W.T. Swank. 1994. Effects of long-term drought on the hydrology and growth of a white pine plantation in the southern Appalachians. For.Ecol.Man. 64:25-39.

Wang, T., A. Hamann, D.L. Spittlehouse, and S.N. Aitken. 2006. Development of scale-free climate data for western Canada for use in resource management. Int.J.Climatology 26:383-397.

Weiner, J. 1990. Asymmetric competition in plant populations. Trends.Ecol.Evol. 5:360-364.

Weiner, J., and S.C. Thomas. 1986. Size variability and competition in plant monocultures. Oikos 47:211-222.

Weiner, J., and C. Damgaard. 2006 Size-asymmetric competition and size-asymmetric growth in a spatially explicit zone-of-influences mode of plant competition. Ecol.Res. 21:770-712.

Westoby, M. 1982. Frequency distributions of plant size during competitive growth of stands: the operation of distribution modifying functions. Ann.Bot. 50:733-735.

Wichmann, L. 2001. Annual variations in competition symmetry in even-aged sitka spruce. Ann. Bot. 88:145-151

Table 6.1. Description of the variables included in the 13 models evaluated by their ability to describe annual changes in competitive symmetry. All models contain age and density, and further variation is described by substituting combinations of variables related to growth rate, spring temperature, growing precipitation, drought, and occurrence of jackpine budworm.

Model	Variables*
1	AGE + DENS
2	AGE + DENS + AVI
3	AGE + DENS + AVI + AVI1
4	AGE + DENS + APRIL
5	AGE + DENS + PREC + PREC1
6	AGE + DENS + APRIL + PREC +PREC1
7	AGE + DENS + CMI
8	AGE + DENS + CMI + CMI1
9	AGE + DENS + APRIL +JPBW + JPBW1
10	AGE + DENS + PREC + PREC1 + JPBW + JPBW1
11	AGE + DENS + APRIL + PREC + PREC1 + JPBW + JBBW1
12	AGE + DENS + CMI + JPBW + JPBW1
13	AGE + DENS + CMI + CMI1 + JPBW + JPBW1

* AGE = stand age, DENS = stem density, AVI = stand volume increment, AVI1 = stand volume increment in the previous year, APRIL = mean april temperature, PREC = annual precipitation, PREC1 = annual precipitation the previous year, CMI = climate moisture index, CMI1 = climate moisture index the previous year, JPBW = presence of jack pine budworm, JPBW1 = presence of jack pine budworm in the previous year.

Table 6.2. A ranking of the 13 apriori models described in Table 6.1, tested by their ability to describe annual changes in the index of competitive symmetry at each of the study plots. Models with an AIC ratio of less than 2 are indicated in bold.

Model	Prince Albert – Rich			Candle Lake – Rich			Flin Flon – Rich			Jenpeg – Rich			Thompson – Rich		
	AIC	Wt	Ratio	AIC	Wt	Ratio	AIC	Wt	Ratio	AIC	Wt	Ratio	AIC	Wt	Ratio
1	**-116.60**	**0.26**	**1.00**	-109.99	0.00	>1000	-24.24	0.05	5.34	-51.55	0.07	5.67	-143.16	0.02	20.08
2	-114.68	0.10	2.61	**-137.66**	**0.69**	**1.00**	-22.28	0.02	14.24	**-55.02**	**0.42**	**1.00**	**-149.16**	**0.45**	**1.00**
3	-113.90	0.07	3.85	-136.05	0.31	2.24	-20.29	0.01	38.45	-53.03	0.15	2.71	**-148.68**	**0.35**	**1.27**
4	**-115.94**	**0.19**	**1.39**	-108.11	0.00	>1000	**-26.26**	**0.14**	**1.95**	-52.22	0.10	4.05	-146.15	0.10	4.51
5	-113.86	0.07	3.92	-109.29	0.00	>1000	**-26.91**	**0.19**	**1.40**	-48.82	0.02	22.25	-139.77	0.00	109.43
6	-112.93	0.04	6.25	-107.49	0.00	>1000	**-27.59**	**0.27**	**1.00**	-50.67	0.05	8.79	-142.30	0.01	30.77
7	-114.72	0.10	2.56	-111.63	0.00	>1000	-22.3	0.02	14.08	-51.56	0.07	5.65	-141.76	0.01	40.42
8	-112.78	0.04	6.73	-109.68	0.00	>1000	-21.24	0.01	23.95	-49.56	0.03	15.36	-139.89	0.00	102.79
9	-113.63	0.06	4.40	-105.90	0.00	>1000	-24.39	0.05	4.96	-49.77	0.03	13.85	-143.90	0.03	13.89
10	-111.59	0.02	12.23	-106.87	0.00	>1000	-25.22	0.08	3.27	-47.16	0.01	50.97	-137.17	0.00	401.27
11	-110.72	0.01	18.90	-105.45	0.00	>1000	**-26.53**	**0.16**	**1.70**	-48.20	0.01	30.22	-140.11	0.00	92.14
12	-112.38	0.03	8.25	-109.62	0.00	>1000	-19.99	0.01	44.66	-49.61	0.03	14.98	-139.22	0.00	143.62
13	-110.45	0.01	21.62	-107.64	0.00	>1000	-19.08	0.00	70.34	-47.61	0.01	40.63	-137.31	0.00	373.45
Model	Prince Albert – Poor			Candle Lake – Poor			Flin Flon – Poor			Jenpeg – Poor			Thompson – Poor		
	AIC	Wt	Ratio	AIC	Wt	Ratio	AIC	Wt	Ratio	AIC	Wt	Ratio	AIC	Wt	Ratio
1	-69.24	0.00	>1000	-161.84	0.00	>1000	-56.01	0.06	4.83	**-38.89**	**0.14**	**1.96**	-169.84	0.00	>1000
2	**-87.57**	**0.35**	**1.89**	**-189.89**	**0.62**	**1.00**	-56.37	0.07	4.02	**-40.23**	**0.27**	**1.00**	**-188.37**	**0.71**	**1.00**
3	**-88.84**	**0.65**	**1.00**	**-188.92**	**0.38**	**1.62**	**-59.16**	**0.27**	**1.00**	**-40.22**	**0.27**	**1.01**	-186.54	0.29	2.51
4	-67.99	0.00	>1000	-159.84	0.00	>1000	-57.24	0.10	2.61	-36.89	0.05	5.31	-168.10	0.00	>1000
5	-65.24	0.00	>1000	-159.03	0.00	>1000	-53.62	0.02	15.95	-37.40	0.07	4.11	-167.57	0.00	>1000
6	-64.01	0.00	>1000	-157.04	0.00	>1000	-55.81	0.05	5.34	-35.52	0.03	10.52	-165.95	0.00	>1000
7	-67.31	0.00	>1000	-160.42	0.00	>1000	-54.77	0.03	8.98	-37.79	0.08	3.39	-168.86	0.00	>1000
8	-65.31	0.00	>1000	-158.56	0.00	>1000	-54.72	0.03	9.20	-37.15	0.06	4.67	-167.04	0.00	>1000
9	-67.07	0.00	>1000	-156.84	0.00	>1000	-57.71	0.13	2.06	-32.95	0.01	38.15	-164.75	0.00	>1000
10	-63.54	0.00	>1000	-155.90	0.00	>1000	-54.16	0.02	12.14	-33.47	0.01	29.44	-164.42	0.00	>1000
11	-63.08	0.00	>1000	-154.06	0.00	>1000	-57.75	0.13	2.03	-31.56	0.00	76.32	-162.78	0.00	>1000
12	-65.60	0.00	>1000	-157.40	0.00	>1000	-54.93	0.03	8.28	-33.81	0.01	24.72	-165.72	0.00	>1000
13	-63.63	0.00	>1000	-155.52	0.00	>1000	-55.61	0.05	5.89	-33.20	0.01	33.67	-163.93	0.00	>1000

Table 6.3. Regression coefficients for model 2 from Table 6.1, which was the most generally supported for describing annual changes in the index of competitive symmetry at the ten jack pine plots in this study. This model predicted the index of competition symmetry as a function of age (AGE), density (DENS), and annual volume growth rate (AVI).

	Prince Albert – Rich		Candle Lake – Rich		Flin Flon – Rich		Jenpeg – Rich		Thompson – Rich	
	β	SE β	β	SE β	β	SE β	β	SE β	β	SE β
AGE*	4.43	0.52	2.23	0.64	1.61	2.27	4.23	1.06	1.79	0.77
DENS	0.09	0.01	0.08	0.04	0.02	0.03	0.11	0.03	0.07	0.04
AVI	0.43	1.54	9.39	1.46	0.79	4.24	7.50	3.25	5.55	1.90
CCF**	0.53		0.72		0.18		0.62		0.49	
RSE***	0.09		0.08		0.34		0.27		0.14	
	Prince Albert – Poor		Candle Lake – Poor		Flin Flon – Poor		Jenpeg – Poor		Thompson – Poor	
	β	SE β	β	SE β	β	SE β	β	SE β	β	SE β
AGE	5.14	0.86	1.61	0.54	2.11	1.29	2.12	1.47	1.62	0.35
DENS	0.18	0.03	0.03	0.02	0.01	0.01	0.02	0.03	0.01	0.01
AVI	12.81	2.64	9.62	1.43	9.64	5.28	11.16	5.67	14.88	2.98
CCF	0.73		0.71		0.34		0.34		0.62	
RSE	0.13		0.07		0.21		0.28		0.05	

*All coefficient values are x 10^{-2}

**1st differenced cross correlation function of observed and model predicted values

***Residual standard error

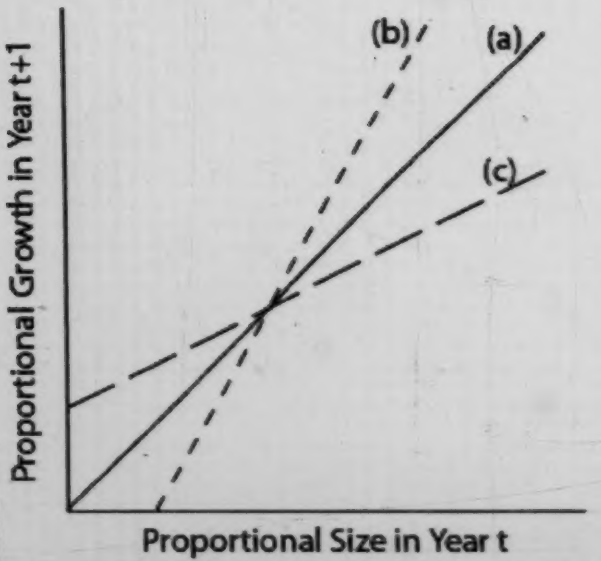

Figure 6.1. Plot of the proportional growth of each tree in year t+1 against the proportional size of each tree in year t and how it is used as index of competitive symmetry. The slope of the regression line indicates relative size symmetry of growth: (a) slope=1, competition is relatively size symmetric, (b) slope>1, competition is positively size asymmetric, and (c) slope<1, competition is negatively size asymmetric.

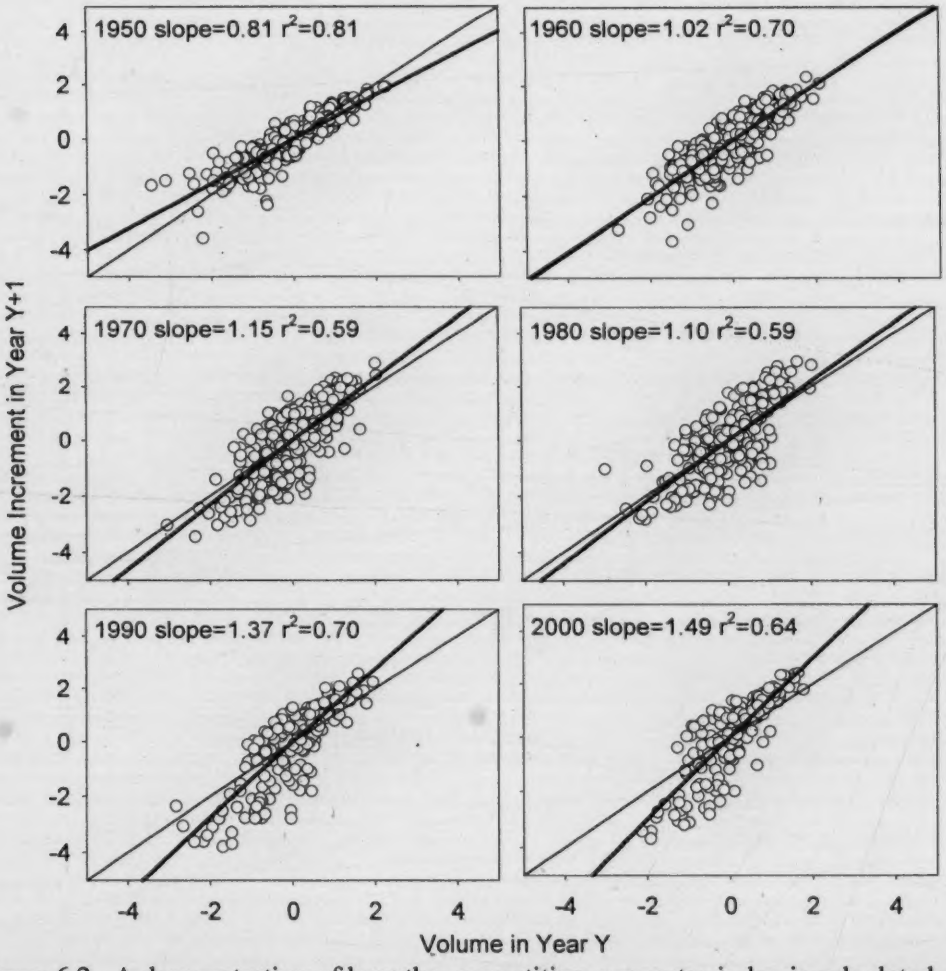

Figure 6.2. A demonstration of how the competition symmetry index is calculated, using data at six time decadal intervals from the poor site at Thompson. Volume and volume increment were both transformed to centered-log ratios. The thick line is the best fitting regression line. The thin line is the line of equality, indicating symmetric competition.

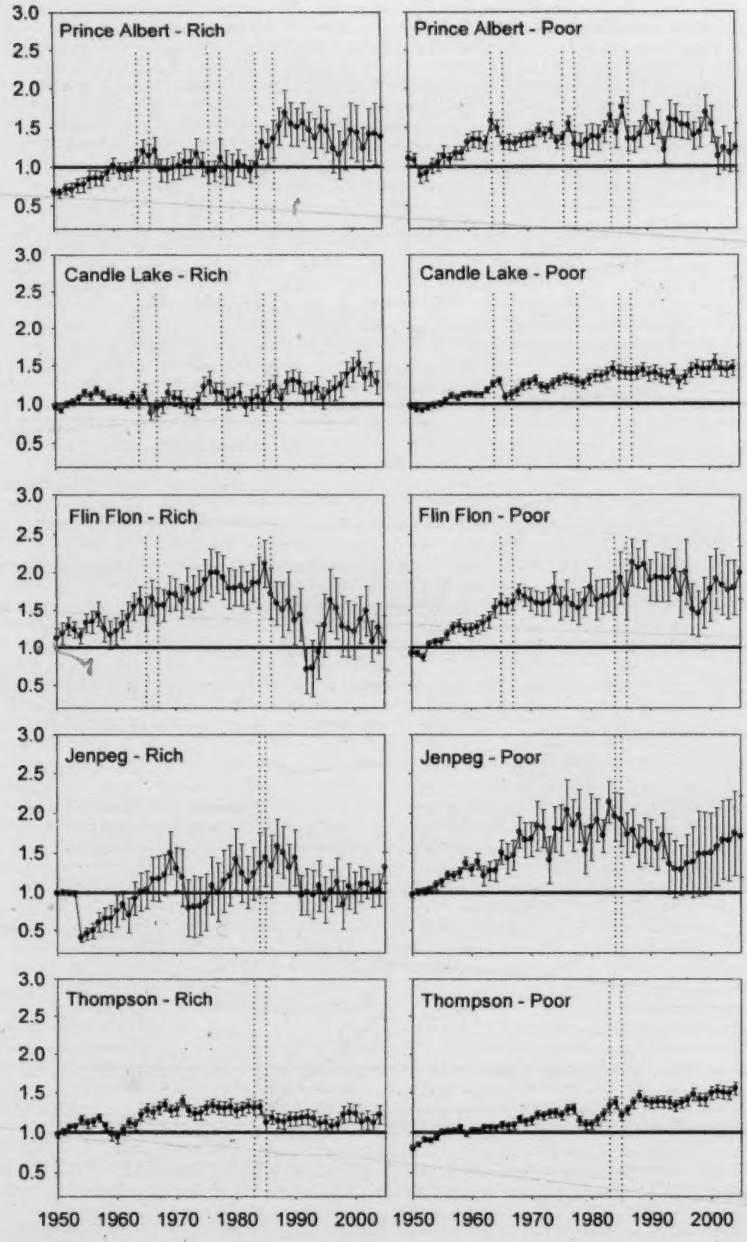

Figure 6.3. Annual trajectories of the index of competitive symmetry index (± SE) since 1950 at each study plot. An index value of one indicates symmetric competition, a value greater than one positive asymmetric competition (large trees grow disproportionately more), and a value less than one negative asymmetric competition (small trees grow disproportionately more). Dashed lines indicate periods of defoliation at each site.

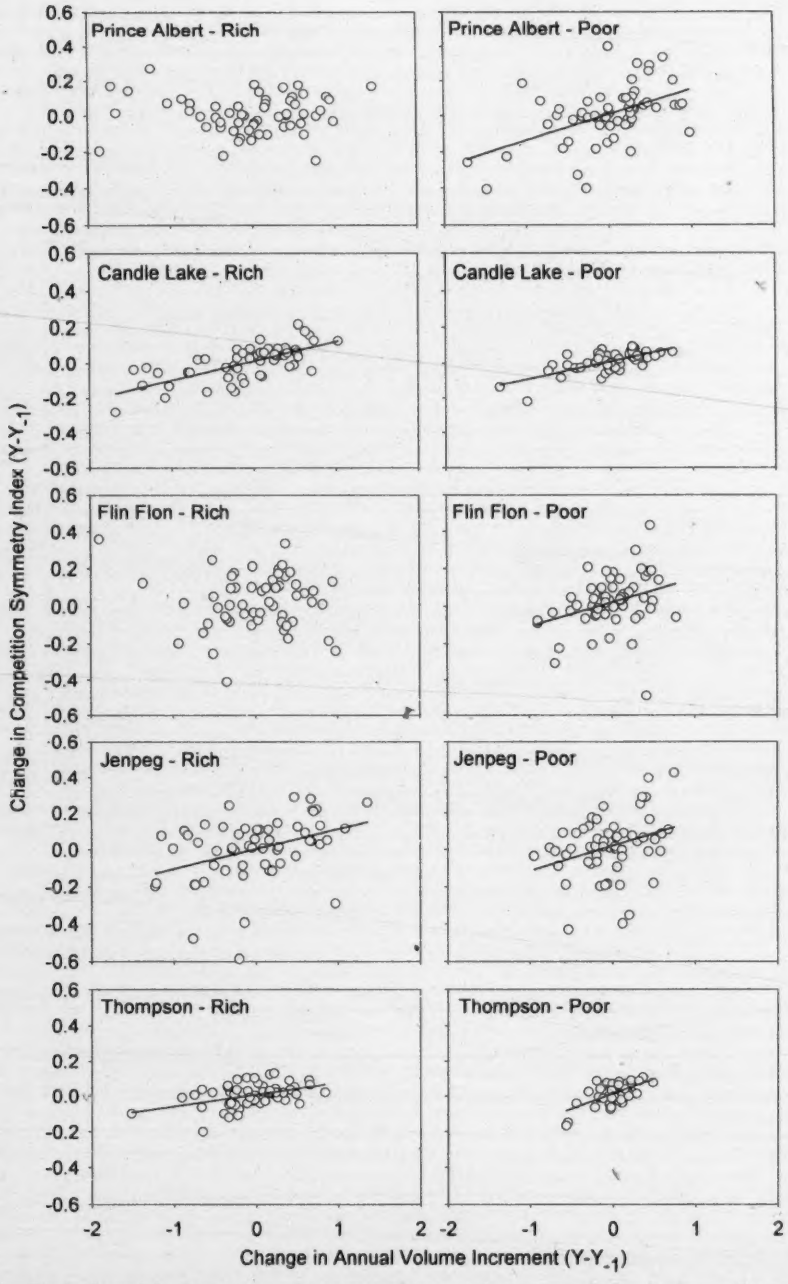

Figure 6.4. Relationship between the annual growth rate and the index of competitive symmetry at each plot, when each is expressed as the change from year Y-1 to year Y. Significant ($p<0.05$) relationships are plotted.

7.0 Annual changes in the spatial distribution of *Pinus banksiana* stands: does pattern fit competition theory?[1]

Studies of the sspatial pattern of forest stands have found random (e.g. Getis and Franklin 1987, Szwagrzyk and Czerwczak 1993), regular (e.g. Kenkel 1988, Chapin et al 1989), or clustered patterns (e.g. Payandeh 1974, Martens et al 1997). From these observed patterns, inferences are made about the processes affecting stand development. However, the spatial pattern of trees also changes over time (Peet and Christensen 1987, Hughes 1988). Most commonly, the pattern shifts from an initially clustered distribution first to a random distribution and then to a regular distribution (Leps and Kindlmann 1987, Ward et al 1996, Kenkel et al 1997). This trajectory of change is usually attributed to density dependent mortality caused by competition with neighbours (Leps and Kindlmann 1987, Chapin et al 1989, Kenkel et al 1997). However, depending upon their importance, external factors may also influence mortality independently of density to produce changes in spatial pattern that do not match the trajectory predicted by competition.

Temporal changes in spatial patterns have previously been studied using periodic measurements from long-term permanent sample plots (e.g. Ward et al 1996, Kenkel et al 1997, Wolf 2005). In this chapter, I use the tree-ring data that I collected to examine annual changes in the spatial patterns of live and dead trees at my study plots. The spatial dynamics of jack pine stands has previously been studied in pure (Kenkel 1988, Kenkel et al 1997) and mixed (Little 2002, Béland et al 2003) stands. However, these studies have either looked at only either a snapshot of spatial patterns from a survey done at a single point in time, or from repeated measurements of permanent plots taken at 10 year intervals. At this time, no other studies have used annual stand reconstruction data to assess temporal changes in spatial patterns. Here, I examine the annual changes in spatial pattern, and therefore am able to investigate the temporal rate of change in spatial pattern. I also relate changes in spatial pattern to the temporal progression of stand development, and investigate the impact of factors like defoliation (Volney 1998) or root disease (Mallett and Volney 1990) that may cause changes in the observed spatial pattern independently of competition.

I hypothesize that the initial distribution of live trees should be clustered because previous studies have found clustered distributions of individuals in young jack pine stands (Payandeh 1974, Kenkel 1988, Kenkel et al 1997), perhaps as a result of spatial variability in seedbed after fire (Miyanishi and Johnson 2002). Over time, the spatial pattern should go through a random phase and eventually reach regularity if density-dependent mortality progresses as expected (Leps and Kindlmann 1987, Peet and Christensen 1987, Ward et al 1996, Kenkel et al 1997). I also hypothesize that, conditional upon the distribution of all trees, dead trees will initially be clustered as mortality should initially occur in locally dense regions, and that the distances at which

---

[1] A version of this chapter has been submitted for publication. Metsaranta, J.M., and Lieffers, V.J. (in review) Annual changes in the spatial distribution of *Pinus banksiana* stands: does pattern fit competition theory? Submitted to Plant Ecology

dead trees are clustered should match the distance of clustering of live trees. Finally, I examine how temporal changes in the spatial scale of spatial interaction are related to population factors like stand density and mortality rate, and also to external disturbance factors like periodic defoliation by jack pine budworm.

7.1 Methods

7.1.1 Field and laboratory.

Field and laboratory methods were as described in previous chapters. In this chapter, spatial data are required, so I only use data from the stem mapped 900 m^2 plots at Candle Lake and Thompson.

7.1.2 Data analysis – spatial patterns

I analyzed the spatial pattern of tree locations using Ripley's K-function (Ripley 1976). This approach allows the determination of spatial pattern at various scales (distances), by comparing the number of neighbours at circles of radius t centered on each individual to the number expected if the individuals followed exhibited complete spatial randomness (CSR). The K-function is usually estimated as:

$$\hat{K}_{(t)} = A \sum_{\substack{i=1 \\ i \neq j}}^{n_1} \sum_{\substack{j=1 \\ j \neq i}}^{n_2} w_{ij} I_t(d_{ij}) / n^2 \qquad (7.1)$$

where n is the number of trees, t is a given radius, A is the area of the plot, d_{ij} is the distance between two points i and j, I_t is a function that takes on the value of 1 if $d_{ij} \leq t$ and 0 otherwise, and w_{ij} is a weighting factor for edge effects. I used the usual square root transformation to the K-function, known as the L(t) function, to stabilize its variance and give it a zero expectation under the hypothesis of complete spatial randomness (CSR):

$$\hat{L}(t) = \sqrt{\frac{K(t)}{\pi}} - t \qquad (7.2)$$

I also analyzed the spatial distribution of live and dead trees using the bivariate K_{12}-function (Lotwick and Silverman 1982). The K_{12}-function is defined as the expected number of points of type 2 (in this case, dead trees) that are located within a given distance t of an arbitrary point of type 1 (in this case, live trees), divided by the intensity, λ_2,of points of type 2, and is estimated from:

$$\hat{K}_{12(t)} = A \sum_{\substack{i=1 \\ i \neq j}}^{n_1} \sum_{\substack{j=1 \\ j \neq i}}^{n_2} w_{ij} I_t(d_{ij}) / n_1 n_2 \qquad (7.3)$$

$$\hat{K}_{21(t)} = A\sum_{\substack{i=1 \\ i\neq j}}^{n_1}\sum_{\substack{j=1 \\ j\neq i}}^{n_2} w_{ji} I_t(d_{ji})/n_1 n_2 \qquad (7.4)$$

where n_1 and n_2 are the numbers of each type of point and the other components of the equation are as described for the K-function. The two equations are combined to calculate the L_{12}-function:

$$L_{12}(t) = \sqrt{\left[n_1 \hat{K}_{12}(t) + n_2 \hat{K}_{21}(t)\right]/\pi(n_1+n_2)} - t \qquad (7.5)$$

For the L_{12}-function, it is possible to test a null hypothesis of either random labeling or population independence (Goreaud and Pellisier 2003). The appropriate hypothesis in this case is random labeling, which holds the locations of the trees fixed and randomly permutes that labels (living or dead) applied to each tree. Thus, conclusions about the spatial distribution of dead trees are conditional upon the spatial pattern of all trees. Clustering indicates that dead trees tend to occur closer together than what is suggested by the overall spatial pattern of both live and dead trees. Regularity indicates that dead trees occur further apart that what is suggested by the overall pattern of live and dead trees. Randomness indicates that dead trees are a random sample from the overall distribution of all trees.

I tested for significance by generating a 99% confidence envelope using the minimum and maximum value of $L(t)$ and $L_{12}(t)$ at each distance t=0.1 m to t=10 m at intervals of 0.1 m for 99 Monte Carlo simulations. I tested the hypothesis of complete spatial randomness (CSR) for $L(t)$, and random labeling for $L_{12}(t)$. Values of $L(t)$ and $L_{12}(t)$ above the confidence envelope indicate a clustered pattern at a given distance t, values of $L(t)$ and $L_{12}(t)$ within the envelope indicate a random pattern at a given distance t, and values of $L(t)$ and $L_{12}(t)$ below the envelope indicate a regular pattern at a given distance t. I corrected for edge effects using Ripley's (1988) isotropic edge correction method, and used the Spatstat package (Baddeley and Turner 2005) for the R statistical system (R Development Core Team 2007) to perform all of these calculations. I calculated $L(t)$ for each study plot for each year since 1950, based upon the distribution of living trees in a given year. I calculated $L_{12}(t)$ for each study plot for each year since 1960, based upon the distribution of living trees in that year, and the accumulated distribution of all trees that have died up to that point in time. I choose 1950 for the univariate analysis because this is the amount of time into the past that tree-ring techniques can reliably reconstruct the growth of jack pine forests in this region, and 1960 for the bivariate analysis so that enough dead trees had accumulated at each site for $L_{12}(t)$ to be estimated.

7.1.3 Data analysis – stand development

I examined two properties of stand development in relation to changes in the spatial pattern: density, expressed as mean tree spacing, and mortality rate. As I described in chapter 3, cumulative mortality in jack pine is sigmoidal (Yarranton and

Yarranton 1975, Kenkel et al 1997), so I fit a Richards function to the cumulative mortality data from each site:

$$M = a\left(1 - e^{-b \cdot A}\right)^{c} \tag{7.6}$$

where M is cumulative mortality, A is stand age. I estimated parameters *a*, *b*, and *c* using non-linear regression with SYSTAT (Systat Software Inc, Point Richmond, CA), and determined when the maximum mortality rate occurred by setting the second derivative of the Richards function to zero and solving for age:

$$A = \frac{\log(c)}{b} \tag{7.7}$$

7.2 Results

7.2.1 Initial and final spatial pattern

Figure 7.1 plots the locations of live and dead trees at each plot in 1950 and 2004. Significant number of trees died at each plot since 1950. Figure 7.2 plots the value of L(t) relative to t for each plot for the 1950 and 2004 distribution of live trees. In 1950, the poor site at Thompson showed clustering at distances from 0.5 m to about 4 to 6 m, the rich site at Thompson showed clustering at distances from about 3 to 4 m and also from 5 to 6 m, and the poor site at Candle Lake showed clustering at all distances above 0.5 m. By 2004, these patterns disappeared and the distribution of trees at these sites was random at all distances. In both 1950 and 2004, the spatial pattern of trees at the rich site at Candle Lake was essentially random at all distances. Figure 7.3 plots the value of $L_{12}(t)$ relative to t for the 1960 and 2004 bivariate distribution of live and dead trees. In 1960, the spatial distribution of dead trees at the poor site at Thompson shows more clustering than the overall distribution of all trees at distances from 5 to 7 m, and the rich site at Thompson shows more clustering that the overall distribution of all trees at distances around 2 m. By 2004, the spatial distribution of dead trees was random sample of all trees at all distances for both sites. In 1960, the spatial distribution of dead trees at the poor site at Candle Lake shows more clustering than the overall distribution of all trees at distances of 1 to 3 m, and the rich site at Candle Lake shows more clustering than the overall distribution of all trees at 1 m, and again at 5 to 7 m. Again, by 2004, the distribution of dead trees at both sites was a random sample of all trees at all distances.

7.2.2 Annual change in spatial pattern

Figure 7.4 plots the temporal trajectory of the significance of L(*t*) for each plot. Significant initial clustering is evident at distances of 0 to 5 m for the poor site at Thompson, at distances from 3 to 6 m for the rich site at Thompson, and at distances from 1 to 3 m and again at 5 m for the poor site at Candle Lake. At the rich site at Thompson and the poor site at Candle Lake, this disappears completely and suddenly around 1970, after which the distribution at the rich site at Thompson remains random until the present. At the poor site at Candle Lake, sporadic regularity begins to appear in

1980, at a distance of about 3.5 m. Clustering is reduced more slowly for the poor site at Thompson, but disappears in 1985. No significant regularity appears at this site. The rich site at Candle Lake shows sporadic clustering in the initial distribution. This disappeared by 1955, after which the distribution is random over all distances.

Figure 7.5 plots the temporal trajectory of the significance of $L_{12}(t)$ for each plot. Significant initial clustering of dead trees, relative to the distribution of all trees, occurred between 1960 and 1980 at distances of 5 to 7 m for the poor site at Thompson 1 to 2 m for the rich site at Thompson, 0 to 4 m for the poor site at Candle Lake, and at 1 m and again at 4 to 8 m for the rich site at Candle Lake. The degree of clustering declined over time. For the poor site at Thompson, it is greatly reduced after about 1980, and begins to appear again sporadically after 1990 at distances around 1 m. For the rich site at Thompson, it disappeared entirely and suddenly around 1975 and did not reappear. For the poor site at Candle Lake, it was greatly reduced after 1980, and thereafter appeared sporadically at distances of around 3 m. It disappeared around 1975 at the rich site at Candle Lake, appeared again sporadically at distances around 1 m until 1990, after which it did not reappear.

By comparison to Figure 7.4, Figure 7.5 shows that the distances at which dead trees are clustered relative to all trees is different than the distances over which the clustering of live trees occurs. The distances at which all trees are clustered are the distances at which dead trees are essentially a random sample of all trees. Most clustering of live trees at the poor site at Thompson occurs at distances of 0 to 6 m, while dead trees are more clustered than all trees at distances from 4 to 8 m. For the rich site at Thompson, most clustering of live trees occurs at distances of 4 to 6 m, while dead trees are more clustered than all trees from 0 to 2 m. Similarly, for the poor site at Candle Lake, clustering of live trees occurs at 4 to 10 m, while dead trees are more clustered than all trees at 0 to 4 m. For the rich site at Candle Lake, dead trees are more clustered than all trees at both 1 to 2 m and 4 to 8 m, even though the distribution of live trees is random.

7.2.3 Spatial pattern in relation to stand development

Based on the derivative of the Richards function fit to the cumulative mortality at each site, I determined that the mortality rate reached a peak in 1970 at each site except the poor site at Thompson, where it peaked in 1975. At the rich site at Thompson and the poor site at Candle Lake, this is also the time that the distribution of living trees shifted suddenly to a random distribution at all distances (Figure 7.4). At the poor site at Thompson, the shift to a random distribution did not precisely correspond to the timing of the peak mortality rate in 1975. This occurred later, in about 1985. The peak mortality rate at the rich site at Candle Lake does not correspond to any change in the spatial distribution. There were no clear relationships between the timing of peak mortality and the spatial distribution of dead trees relative to all trees, except that the spatial distribution of dead trees relative to all trees becomes random somewhat after mortality peaks at each site.

In Figure 7.6, I plot how the mean spacing of live trees changes over time at each site, and identify the approximate time at which the spatial distribution of live trees at each time becomes random, based on Figure 7.4. The shift from a clustered distribution to a random distribution occurs at a similar mean spacing at each site. This shift occurs in 1985 at a mean tree spacing of 2.1 m at the poor site at Thompson, in 1970 at a mean tree spacing of 2.4 m at the rich site at Thompson, in 1970 at a mean tree spacing of 2.1 m at the poor site at Candle Lake, and in 1955 at a mean tree spacing of 2.3 m at the rich site at Candle Lake. The spacing at which this shift occurs was on average 2.23 m, representing a stand density of about 2020 trees ha^{-1}. There were no clear relationships between tree spacing and changes in the distribution of live and dead trees.

7.3 Discussion

Few common trends were found at all four sites. Spatial pattern of live trees shifted from a clustered distribution to a random distribution at an average spacing of 2.23 m, which is near the mean crown width for mature jack pine in this region (Halliwell and Apps 1997). The initial distributions dead trees relative to all trees were at least somewhat clustered initially at all sites. This clustering always declined over time and disappeared, meaning that eventually dead trees were simply a random sample of all trees. However, all other aspects of the spatial development varied enough to conclude that none followed the same pattern. These stands have little structural diversity and seemingly little room for possible variation in stand trajectories, so this variability was surprising

The initial distances at which live trees were clustered differed at each site. This was most likely due to spatial variation in the distribution of suitable seed bed at stand initiation (Miyanishi and Johnson 2002). This clustering either: declined steadily, disappeared suddenly at the same time as mortality peaked, or was never really present at all. Significant regularity only appeared at the poor site at Thompson, so the hypothesis that competition leads to a regular distribution of trees (Peet and Christensen 1987, Hughes 1988, Chapin et al 1989) was not strictly supported. Dead trees were clustered relative to all trees at different distances than live trees were clustered. These should have been the same if mortality driven by competition with neighbours occurred first in the highest density patches (Kenkel et al 1997). That they are not suggests that density-independent factors are causing mortality at a different spatial scale (Szwagrzyk and Czerwczak 1993). Simulation studies of temporal changes in spatial pattern have found that when mortality depends on neighbours, clustered patterns first become random and then regular over time and that random patterns also become regular over time (Leps and Kindlmann 1987). When mortality does not depend on neighbours, random patterns stay random over time (Kent and Dress 1979), and both clustered and regular patterns also become random (Kent and Dress 1980). At two of the four sites clustered initial patterns became random but did not become regular, and at one site an essentially random initial pattern remained random. Only the appearance of regularity from an initially clustered or random pattern indicates that mortality depends upon neighbours, suggesting that mortality in this study did not generally depend upon neighbours.

Kenkel (1988) found that an initially clustered distribution in a jack pine stand shifted to a regular distribution at short distances and that the distribution of dead trees was a random sample of trees from the initial pattern at all distances. In another study, Kenkel et al (1997) found that clustering at a jack pine stand declined over time, but did not reach significant regularity. To the best of my knowledge, the four sites considered in this study, combined with the sites studied in Kenkel (1988) and Kenkel et al (1997), are the only pure jack pine stands where temporal changes in the spatial pattern of jack pine stands have been studied in detail. Taken together, all of these results suggest that convergence to regularity is not a universal aspect of the dynamics of jack pine. Some commonalities exist, but the dynamics are variable enough to say that all sites likely follow different patterns of spatial development. It is most likely that site-specific interactions between density dependent and independent processes are causing this variability.

The poor sites most closely matched the hypothesized pattern of stand development. If asymmetric above ground competition for light primarily drives these changes, then these sites should not have shown these patterns because they had low productivity, small trees and low crown closure. Competition should have been symmetric and below ground. Thus, although the mode of above and below ground competition is different (Schwinning and Weiner 1998), it may be that the patterns that they produce in this forest type are indistinguishable. At the poor site at Candle Lake, clustering disappeared suddenly around 1970, three years after a significant jack pine budworm outbreak in this region (Volney 1988), and at the same time that mortality peaked. Mortality tends to lag some years after the end of jack pine budworm outbreaks (Volney 1998), so the spatial dynamics of this site were likely influenced by this density independent factor. However, since jack pine budworm defoliation causes greater mortality in suppressed trees than dominant trees (Gross 1992), its effect may also be indistinguishable from that of competition.

The distribution of living trees at the rich site at Candle Lake was essentially always random. The density of this stand was the lowest of all four sites, meaning that trees here were least likely to interact. Kashian et al (2005) have shown that local variation in density at the time of establishment strongly influences the rate at which stands develop. Many trees had the remains of large branches low on the bole, indicating that this stand always had a low density, possibly because many of the large gaps in this stand contain dense clusters of green alder (*Alnus viridis* var. *crispa*) in the understory. The presence of this shrub interacts with density and soil moisture to determine the site productivity of jack pine forests in this region (Vogel and Gower 1998), possibly in a way that influences the spatial distribution of trees at stand initiation. Despite having a random distribution, initial mortality at the rich site at Candle Lake was clustered. Root rot was present in many nearby stands, and the growth increment at this site was nearly the same as at the poor Candle Lake site since about 1970, despite being more than double the rate before that time. This region experienced a significant outbreak of jack pine budworm from 1964-1967 (Volney 1988). Trees weakened by defoliation may have become more susceptible to root rot (Mallett and Volney 1990), and it is likely the interaction of these two factors that led to the observed spatial pattern of mortality at this site, despite the random initial pattern of live trees. Clustering at the rich site at

Thompson also disappeared suddenly in 1970. The reason for this is unclear because historical reports of the Canadian Forest Insect and Disease Survey suggest that the jack pine budworm outbreak occurring from 1964-1967 did not occur in northern Manitoba, tree-ring data from the site do not show a growth decline during that period, and no obvious evidence of root rot was found at this or nearby stands. However, this stand also contained clusters of alder shrubs, and had evidence of originating at a low density. No clearly dominant process was affecting the observed spatial pattern at this site.

Previous studies suggest that the development of jack pine stands has an early density independent phase with two-sided competition for soil resources that results in clusters of suppressed trees in locally dense areas, followed by a later phase of one-sided competition where these suppressed trees are shaded out by their larger neighbours (Kenkel 1988, Kenkel et al 1997, Little 2002). The results of this study suggest that density-independent factors causing mortality may be equally as important in influencing the dynamics of these stands. These include defoliation (Volney 1998), windthrow (Elie and Ruel 2005), drought (Yarranton and Yarranton 1975) or root disease (Mallett and Volney 1990). Other factors such as spatial genetic structure (Xie and Knowles 1991, Xie and Knowles 1992), variable seedbed quality (Thomas and Wein 1990, Miyanishi and Johnson 2002), or local variability in density (Kashian et al 2005) may also affect the rate at which stand development processes occur right from the point of stand initiation, and may predetermine the potential pathways that a given stand could follow over its lifetime. These processes could dominate competition after the point of peak mortality has passed, are likely occurring even as mortality rates are high, and may begin as early as stand initiation at sites where genetic, microsite or density variation are high. Similar studies in more stands may elucidate a small number of spatial development pathways where either competition or other factors dominate at different times in stand development. Presently, however, the large number of interacting factors that may play a role in influencing these pathways make it impossible to predict how many exist, which a given stand has followed in the past or which it might follow in the future. Even in these simple jack pine stands, realized patterns of stand development are more complex than what is predicted by competition alone.

7.4 Literature Cited

Baddeley, A., and R. Turner. 2005. Spatstat: an R package for analyzing spatial point patterns. J.Stat.Soft. 12:1-42.

Béland, M., J-M. Lussier, Y. Bergeron, M-H. Longpre, and M. Béland. 2003. Structure, spatial distribution and competition in mixed jack pine (*Pinus banksiana*) stand on clay soils of eastern Canada. Ann.For.Sci. 60:609-617.

Chapin III, F.S. J.B. McGraw, and G.R. Shaver. 1989. Competition causes regular spacing of alder in Alaskan shrub tundra. Oecologia 79:412-416.

Elie, J-G, and J-C. Ruel. 2005. Windthrow hazard modeling in boreal forests of black spruce and jack pine. Can.J.For.Res. 35:2655-2663.

Getis, A., and J. Franklin. 1987. Second-order neighborhood analysis of mapped point patterns. Ecology 68:473-477.

Goreaud, F., and R. Pelissier. 2003. Avoiding misinterpretation of biotic interactions with the intertype K_{12}-function: population independence vs. random labeling hypotheses. J.Veg.Sci 14:681-692.

Gross, H.L. 1992. Impact analysis for a jack pine budworm infestation in Ontario. Can.J.For.Res. 22:818-831.

Halliwell, D.H., and M.J. Apps. 1997. Boreal Ecosystem-Atmosphere Study (BOREAS) biometer and auxiliary sites: overstory and understory data. Nat.Res.Can., Can.For.Serv., North.For.Cent., Edmonton, AB.

Hughes 1988. Spatial dynamics of self-thinning. Nature 336:521.

Kashian, D.M., M.G. Turner, W.H. Romme, and C.G. Lorimer. 2005. Variability and convergences in stand structural development on a fire-dominated subalpine landscape. Ecology 86:643-654.

Kenkel, N.C. 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. Ecology 69:1017-1024.

Kenkel, N.C., M.L. Hendrie, and I.E. Bella. 1997. A long-term study of *Pinus banksiana* population dynamics. J.Veg.Sci. 8:241-254.

Kent, B.M., and P. Dress. 1979. On the convergence of forest stand spatial pattern over time: the case of random initial spatial pattern. For.Sci. 25:445-451.

Kent, B.M., and P. Dress. 1980. On the convergence of forest stand spatial pattern over time: the case of regular and aggregated initial spatial patterns. For.Sci. 26:10-22.

Leps, J., and P. Kindlmann. 1987. Models of the development of spatial pattern of an even-aged plant population over time. Ecol.Mod. 39:45-57.

Little, L.R. 2002. Investigating competitive interactions from spatial patterns of trees in multi-species boreal forests: the random mortality hypothesis revisited. Can.J.Bot. 80:93-100.

Lotwick, H.W., and B.W. Silverman. 1982. Methods for analyzing spatial processes of several types of points. J.R.Stat.Soc.B. 44:403-413.

Mallett, K.I., and W.J.A. Volney. 1990. Relationships among jack pine budworm damage, select tree characteristics, and *Armillaria* root rot in jack pine. Can.J.For.Res. 20:1791-1795.

Martens, S.N., D.D Breshears, C.W. Meyer, and F.J. Barnes. 1997. Scales of above-ground and below-ground competition in a semi arid woodland detected from spatial pattern. J.Veg.Sci. 8:655-664.

Miyanishi, K., and E.A. Johnson. 2002. Process and patterns of duff consumption in the mixedwood boreal forest. Can.J.For.Res. 32:1285-1295.

Payandeh, B. 1974. Spatial pattern of trees in major forest types of northern Ontario. Can.J.For.Res. 4:8-14.

Peet, R.K., and N.L. Christensen. 1987. Competition and tree death. BioScience 37:586-595.

R Development Core Team. 2007. R: A Language and Environment for Statistical Computing. R foundation for statistical computing, Vienna, Austria. ISBN 3-900051-07-0. URL http://www.R-project.org.

Ripley, B. 1976. The second order analysis of a stationary point process. J.App.Prob. 13:255-266.

Ripley, B. 1988. Statistical Inference for Spatial Processes. Cambridge University Press, Cambridge, UK.

Schwinning, S, and J. Weiner. 1998. Mechanisms determining the degree of size symmetry in competition among plants. Oecologia 113:447-455.

Szwagrzyk, J., and M. Czerwczak. 1993. Spatial patterns of trees in natural forests of East-Central Europe. J.Veg.Sci. 4:469-476.

Thomas, P.A., and R.W. Wein. 1990. Jack pine establishment on ash from wood and organic soil. Can.J.For.Res. 20:1926-1932.

Vogel, J.G., and S.T. Gower. 1998. Carbon and nitrogen dynamics of boreal jack pine stands with and without a green alder understory. Ecosystems 1:386-400.

Volney, W.J.A. 1988. Analysis of historic jack pine budworm outbreaks in the Prairie provinces of Canada. Can.J.For.Res. 18:1152-1158.

Volney, W.J.A. 1998. Ten-year tree mortality following a jack pine budworm outbreak in Saskatchewan. Can.J.For.Res. 28:1784-1793.

Ward, J.S., G.R. Parker, and F.J. Ferrandino. 1996. Long-term spatial dynamics in an old-growth deciduous forest. For.Ecol.Man. 83:189-202.

Wolf, A. 2005. Fifty year record of change in tree spatial patterns within a mixed deciduous forest. For.Ecol.Man. 215:212-223.

Xie, C.Y., and P. Knowles. 1991. Spatial genetic substructure within natural populations of jack pine (*Pinus banksiana*). Can.J.Bot. 69:547-551.

Xie, C.Y., and P. Knowles. 1992. Associations between allozyme phenotypes and soil nutrients in a natural population of jack pine (*Pinus banksiana*). Biochem.Syst.Ecol. 20:179-185.

Yarranton, M, and G.A. Yarranton. 1975. Demography of a jack pine stand. Can.J.Bot. 53:310-314.

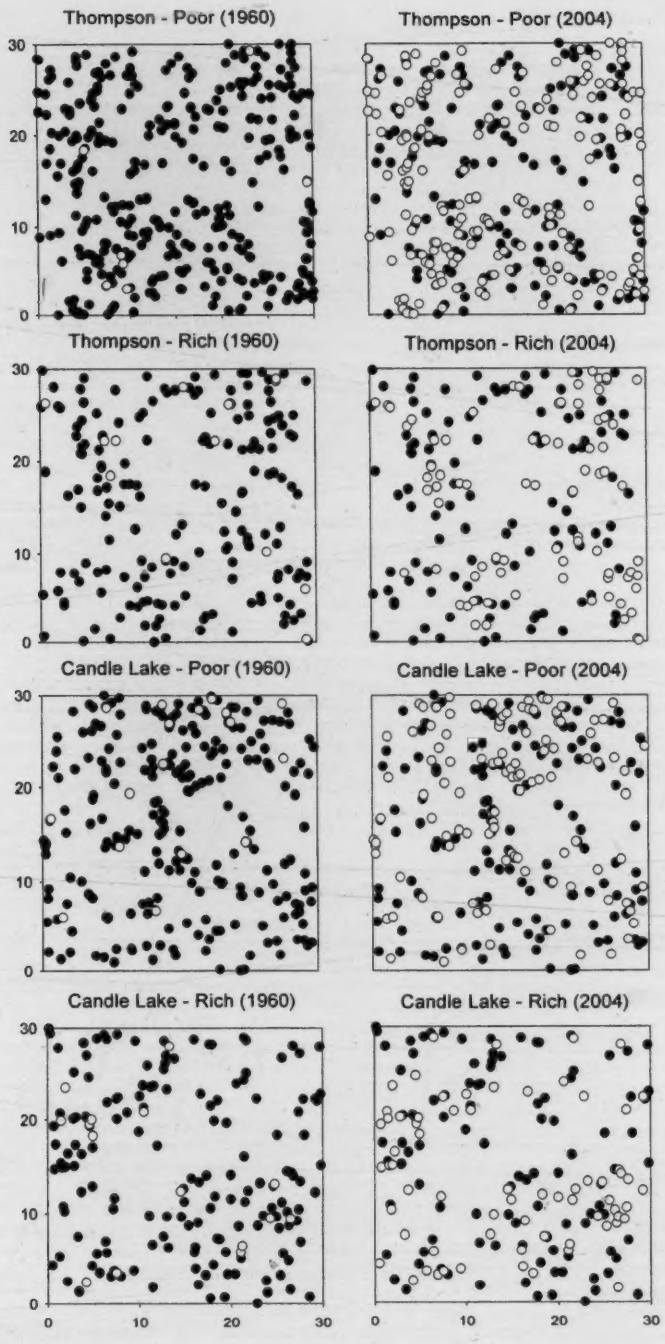

Figure 7.1. Initial and final locations of live (filled circles) and dead (open circles) trees at each study plot.

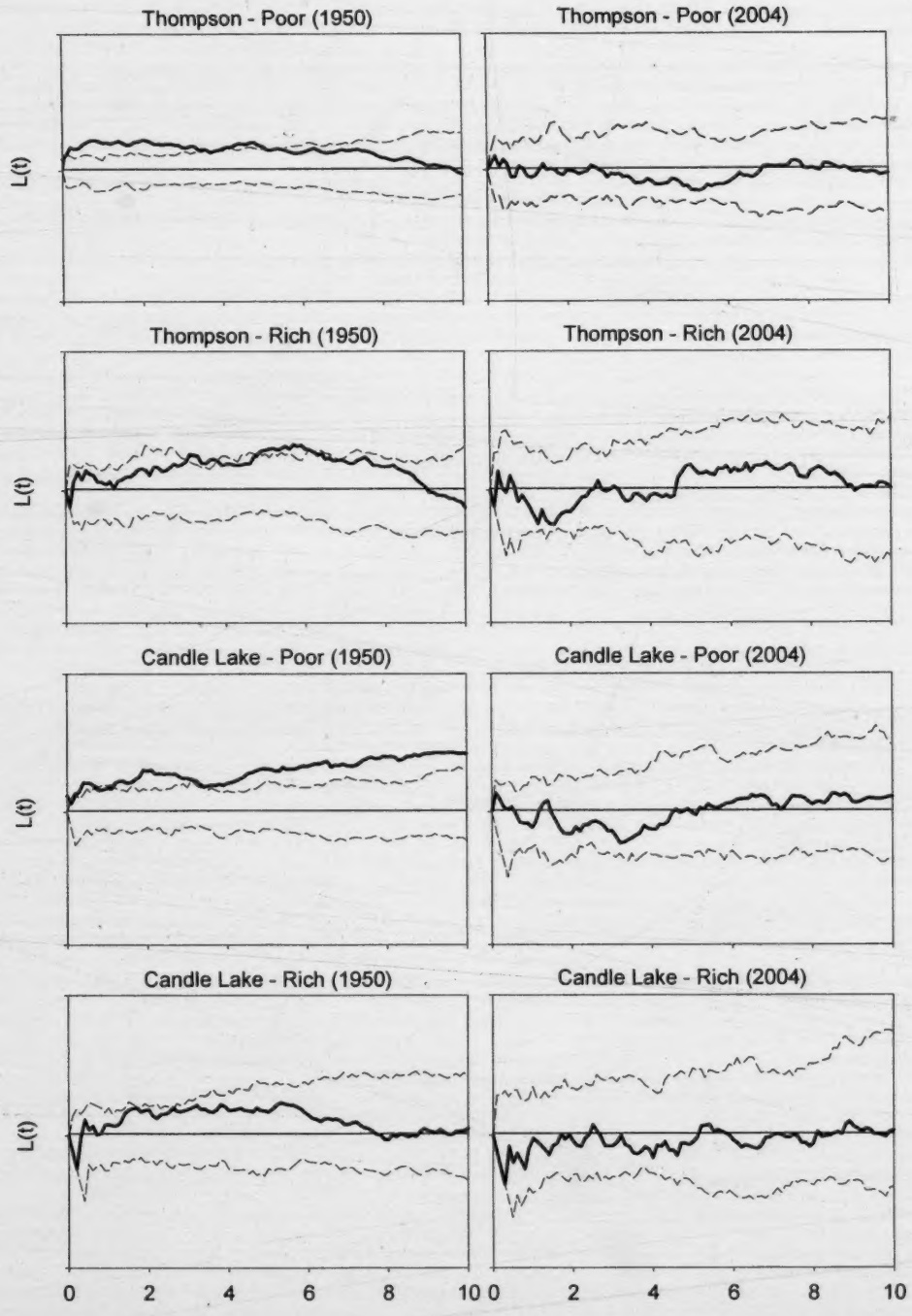

Figure 7.2. Plots of the L(t) function for living trees in 1950 and 2004 at each study plot along with 99% confidence envelope for distances of t=0 to 10 m for the hypothesis of complete spatial randomness. L(t) values above the confidence envelope indicate clustering, and L(t) values below the confidence envelope indicate regularity.

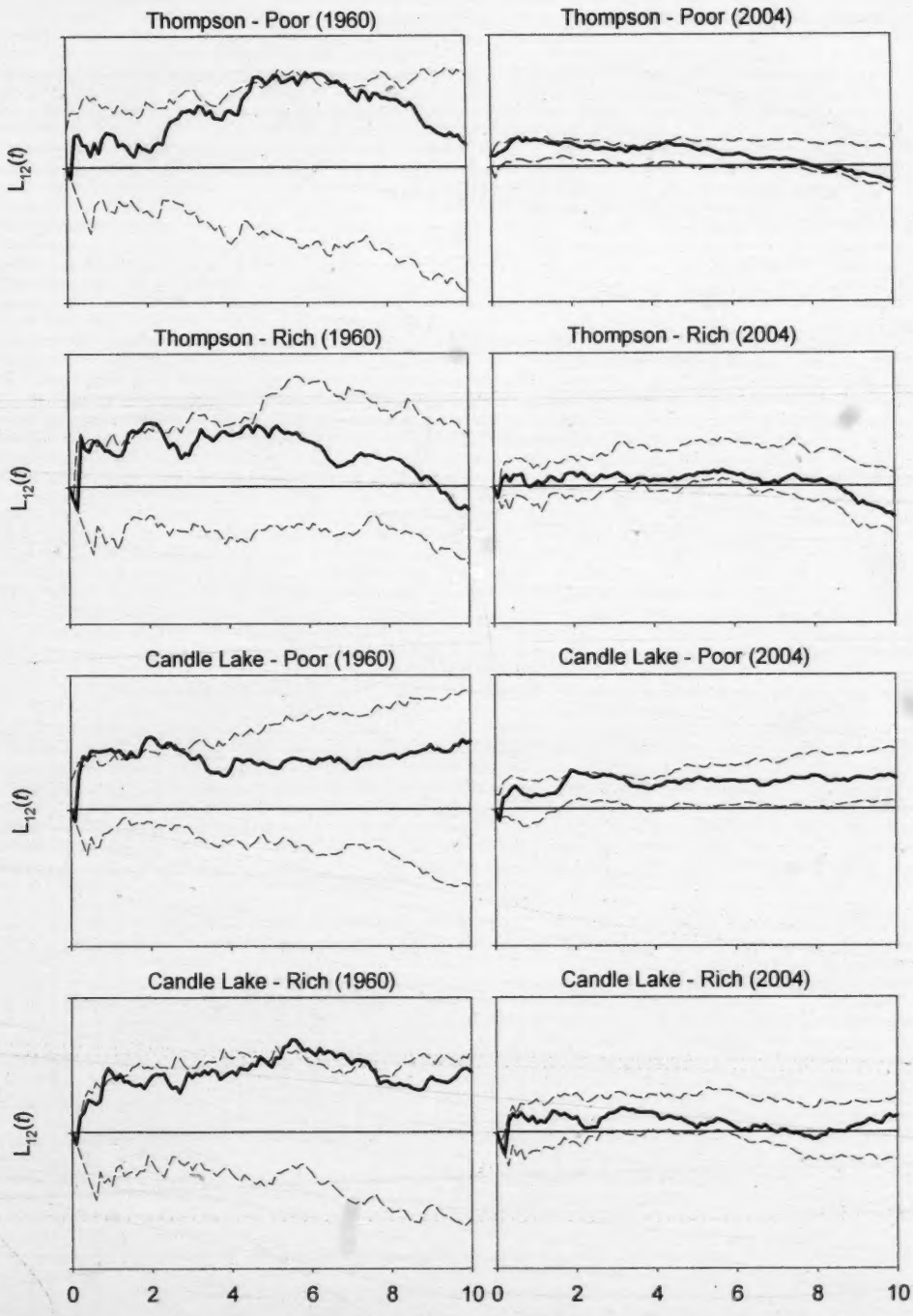

Figure 7.3. Plots of the $L_{12}(t)$ function in 1960 and 2004 at each study plot along with 99% confidence envelope for distances of t=0 to 10 m for the hypothesis of random labeling of live and dead trees. $L_{12}(t)$ values above the confidence envelope indicate clustering relative to the distribution of all trees , and $L_{12}(t)$ values below the confidence envelope indicate regularity relative to the distribution of all trees.

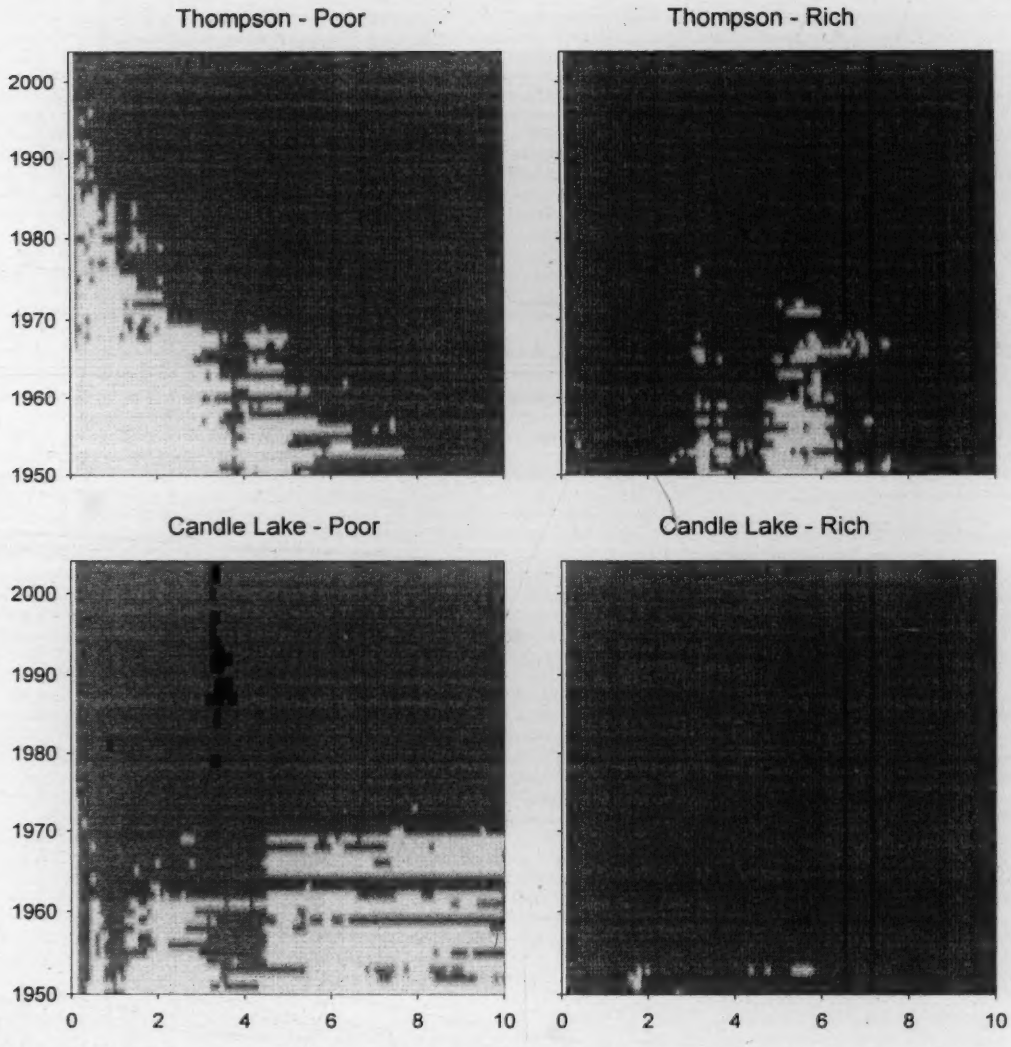

Figure 7.4. Significance of L(t) over time at each site. Time (years) is plotted along the y-axis, and distance from t=0 to 10 m in 0.1 m increments is plotted along the x-axis. Light areas indicate significant clustering, grey areas represent randomness, and dark areas indicate significant regularity.

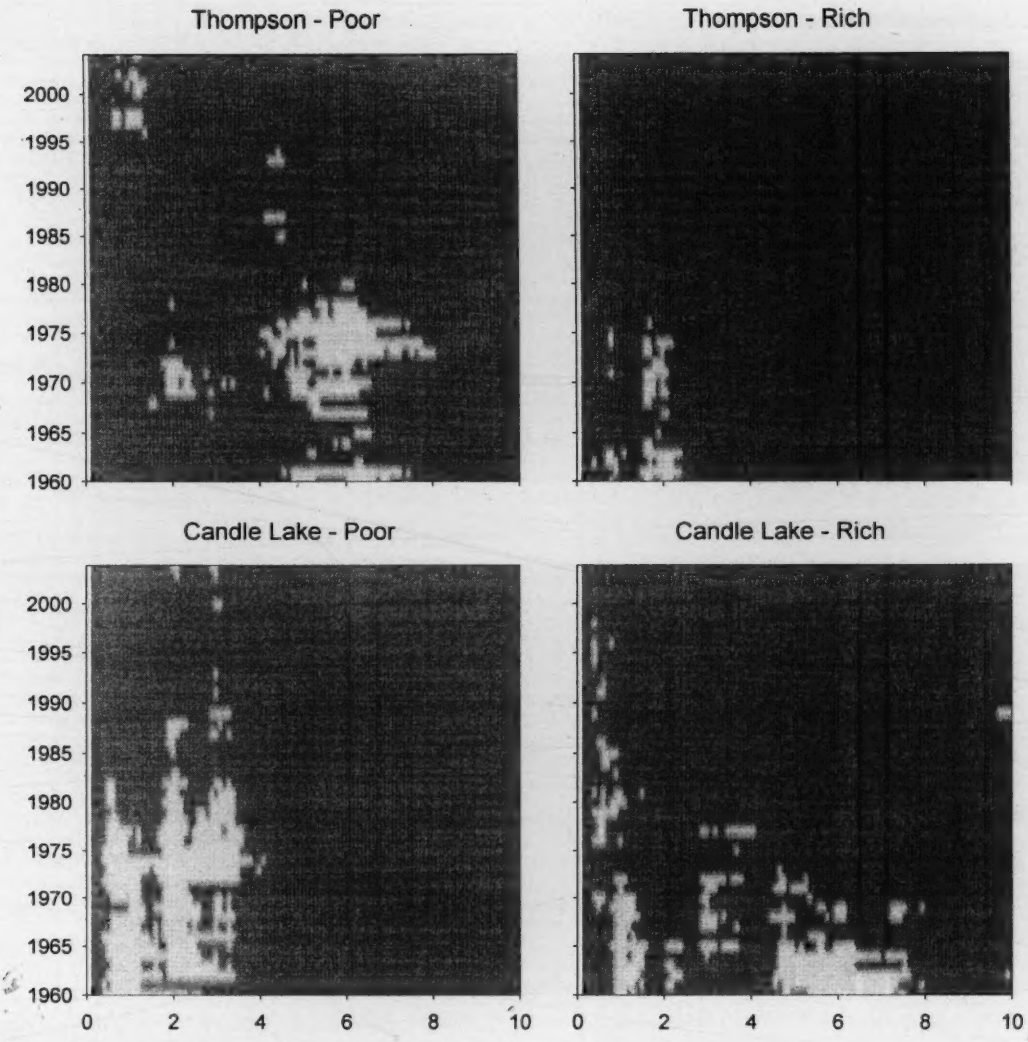

Figure 7.5. Significance of $L_{12}(t)$ over time at each site. Time (years) is plotted along the y-axis, and distance from t=0 to 10 m in 0.1 m increments is plotted along the x-axis. Light areas indicate significant clustering relative to all trees, grey areas represent randomness, and dark areas indicate significant regularity relative to all trees.

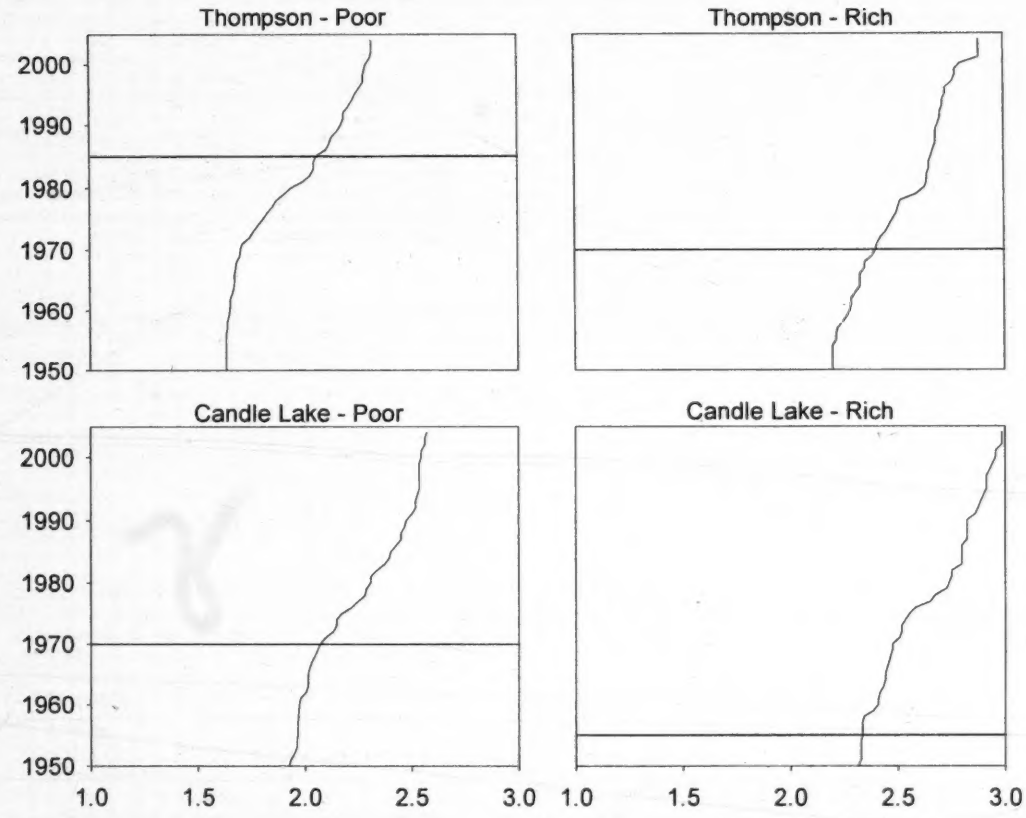

Figure 7.6. Temporal trajectory of mean tree spacing at each site. Time (years) is plotted on the y-axis and mean spacing of live trees (m) on the x-axis. The solid horizontal line represents the approximate time at which the spatial distribution of live trees changes from clustered to random at each site, based on Figure 7.4.

8.0 Conclusions

In this thesis, I used dendroecological methods to reconstruct and investigate the inter-annual variability in growth, competition, and spatial pattern of jack pine forests in Saskatchewan and Manitoba, Canada. I described and evaluated my methods for scaling ring-width data at breast height to tree level volume increment, showed that jack pine stands in this region can be reliably reconstructed for up to 50 years into the past using these methods, and demonstrated that tree-ring stand reconstruction can be a valuable tool for collecting enhanced, annual resolution data on forest growth and stand development. I also took three different approaches to examining annual variation in competition. I first examined size and growth rate independently. I did this by quantifying the inequality of size and size increment using the Gini and Lorenz asymmetry coefficients, and examining how this inequality changed over time in relation to stand development and annual growth rate. I then examined size and growth rate together by assessing their size proportionality (competition symmetry) and how this changed over time, again in relation to stand development, but also to annual variation in growing conditions. I quantified annual variation in growing conditions using (1) the weather variables most commonly correlated with jack pine growth, based on a review of the literature on climate-growth relationships in jack pine, and (2) historical records of insect defoliation. Finally, I undertook a spatial analysis that examined how the distribution of live and dead trees changes annually. I showed that this detailed approach provides some interesting insights into stand development in these forests.

In chapter 2, I showed that even with relatively simple equations, volume increment estimates from partial stem analysis are in the range of error of other mensurational studies, and thus should have yielded results equal to what would have been obtained from full stem analysis in the rest of the analyses. The equations that I used were chosen because I could parameterize them from readily available data, or obtain parameters easily from the extant literature on my study region. In other applications, they could be replaced by equations that are sensitive to the effect of stand conditions and competitive effects on height-diameter relationships (e.g. Sharma and Zhang 2004) or tree taper (e.g. Morris and Forslund 1992, Muhairwe et al 1994), which would result in a small improvement in the volume estimates. Most growth studies use some similar method of scaling breast height data to whole tree growth measures, but rarely are the accuracy of these methods assessed quantitatively. In chapter 3, I further validated my methods by demonstrating that the stand reconstruction techniques that I used can generate annual time series of the mortality of trees in maturing jack pine stands up to about 50 years into the past. This conclusion is based upon the observed timing of mortality, relative to the timing of self-thinning observed in others studies of jack pine and the observed persistence of downed logs relative to the half-life of coarse woody debris observed in previous studies of wood decomposition. As a result, I begin the rest of the analyses that I present in the year 1950, after which losses of trees to decomposition was likely low enough to not bias the results of the rest of my analyses.

In chapter 4, I demonstrated how dendrochronological stand reconstruction techniques can provide data that in some cases are an improvement on those obtained

from the permanent sample plots that are presently used to monitor forest growth and stand development. The data presented in chapter 4 are only a small portion of all the trajectories that could be examined with these data, and were chosen because they represented some of the common uses to which PSP data are put in forest models. By adopting these techniques where appropriate, it would be possible to quickly collect growth and stand development data at an annual resolution, without waiting many years for re-measurement data from conventional PSPs. Presently, many forest models are parameterized using periodic data from PSPs, but may not adequately assess the influence of transient factors like insect defoliation or drought on growth or stand dynamics. With these data, the influence of these transient factors affecting growth and stand dynamics (e.g. Wichmann 2001, Hogg et al 2005, Hogg and Wein 2005, Cooke and Roland 2007) could more thoroughly be assessed and therefore considered in forest management plans. These techniques are presently ready to be applied in forest monitoring programs, and the only further suggestion prior to their adoption would potentially be a cost-benefit analysis that quantifies the additional benefit of annual data, relative to the additional labour associated with extracting, processing, and measuring large numbers of increment core samples.

In chapter 5, I examine size and size increment independently. I used the Gini and Lorenz asymmetry coefficients to quantify their inequality. Previous studies often attribute changes in size inequality to competition, which should be reflected in variables quantifying stand development. Changes in the inequality of size increment, however, have not previously been quantified, and I hypothesized that they would be related to inter-annual variability in stand level growth rate. The results showed that inequality in size was in fact well described by changes in stand development. Inequality of size increment was also related annual growth rate. Size increments were more unequal when growth rates are low. During low growth rate years, the observed inequality in size increment was often primarily due to a few trees with large growth rates. I proposed that size hierarchies are initially established by these small differences in growth during stress years, and hypothesized that these differences are then magnified by asymmetric competition during years with normal growth. In this region, the primary selective agents are likely insect defoliation and drought, and it is likely that these few trees that are able to maintain high growth rates during stress years are better adapted to these selective agents.

In chapter 6, I used an index of competition symmetry that quantified the relative proportionality of size and growth to examine size and size increment concurrently. The results showed that the asymmetry of competition showed both site specific and temporal variability. All plots had periods of time when competition was symmetric, some showed large annual fluctuations in competition symmetry, and a few even had periods of negative asymmetric competition. Previous studies have shown that variation in growing conditions can have differential effects on trees of different size classes, and therefore influence the mode of competition. Based on a review of the literature, I proposed that variation in precipitation, spring temperatures, and defoliation were the main factors influencing variation in growing conditions for jack pine in this region, and tested these variables as predictors of the observed changes in competition symmetry. At most sites, apart from being related to stand development (changes in age and density), variation in

competitive asymmetry was actually best predicted by inter-annual variability in the growth rate, rather than the factors I hypothesized to be associated with variation in growing conditions. Overall, the results showed that when growth rates increased, competition became more asymmetric, and that when growth rates decreased, competition became more symmetric. Though competition may not have reached symmetry in the absolute sense, these results show that in a relative sense, smaller trees may perform better during years of poor growth. Competition indices used in many stand dynamics models generally assign a growth advantage to larger trees, but do not account for the possibility that smaller trees may in fact perform relatively better in some circumstances.

In chapter 7, I examined changes in the spatial distribution of individuals over time. Most previous studies suggest that competition should eventually result in a regular spatial pattern, but this hypothesis wasn't strictly supported. Modeling studies with various assumptions about the influence of neighbours on mortality (Kent and Dress 1979, Kent and Dress 1980, Leps and Kindlmann 1987) suggest that only the actual appearance of regular distributions is suggestive of an influence of neighbours on mortality, since both dependent and independent mortality cause clustered distributions to become random. Here, I only found a regular distribution to appear sporadically at one site. I proposed that this result showed that density-independent factors causing allogenic mortality (Oliver and Larson 1996) may be equally as important as competition with neighbours in influencing the spatial dynamics of these stands, particularly after the point at which the mortality rate has peaked. Similar studies in more stands may elucidate a small number of spatial development pathways where either competition or one or more of these other factors dominate at different times in stand development. Presently, however, the large number of interacting factors that may play a role in influencing these pathways make it impossible to predict how many exist, which a given stand has followed in the past or which it might follow in the future.

Taken together, the results of this thesis suggest that even in these simple jack pine stands, realized patterns of stand development are more complex than what is predicted by competition alone. In fact, some of the results of different parts of this study result in contradictory conclusions that are not easily reconciled. This suggests that the mechanism for explaining the observed differences in competition symmetry, inequality, and spatial patterns in jack pine requires further study. Weiner and Thomas (1986) noted that a comprehensive theory explaining changes in competition in relation to stand development was yet to be discovered. Schwinning and Weiner (1998) further postulated that this theory would need to explain how episodic inputs and deficits of resources influence the mode of competition. The factors that influence variation in resources for a given species differ in different regions (e.g. Hogg et al 2005, Cooke and Roland 2007), and also within regions for a given species (e.g. van Niejenhuis and Parker 1996). As a result, I also suggest that such a theory will need to take into account the adaptation of local plant populations to the selective factors that are most limiting in a given region, as this is likely what determines when specific resources are in deficit or abundance in a given area. The periods of time when this resource are in deficit represent the periods when the ability to compete for this resource are most influential to the variability of individual growth rates.

Much residual variability in the growth response in many forest growth and stand dynamics models is not explained by competition. Inter-annual variation in growing conditions may be the cause of some of this unexplained variability. To date, it has not been possible to incorporate such effects into these competition models because most such studies only measure competition at a single point in time (Burton 1993) and because data at an annual resolution data on the size and growth of both subject and competitor trees are not usually available. Tree growth studies quantify competition effects with various indices (e.g. Lorimer 1983, Tome and Burkhardt 1989, Holmes and Reed 1991, Biging and Dobbertin 1992, Biging and Dobbertin 1995) that typically moderately increase correlations between observed and predicted growth rates when they are used in growth models. The analysis in this thesis showed that the annual growth rate is an important factor that affects several aspects of the competition dynamics. This results in a somewhat circular conclusion, since it is usually assumed that competition is driving growth, and not vice versa. I suggest here that the direction of causality should potentially be reversed. When growth rates are high, competition between plants becomes more intense. As a result, more focus should be placed on determining what environmental factors cause growth rate to vary, and less focus on improving how competition is represented. I also suggest that the observation in many competition studies that larger trees have a growth advantage does not reveal anything about the root causes of why some trees are successful and become large and dominant, while other trees are not successful and become suppressed and eventually die. In some circumstances, which are associated with years of poor growth, small trees may actually perform relatively better. Future research on competitive dynamics in boreal forests should focus on determining the reasons why certain trees initially gain a competitive advantage and the reasons why size hierarchies are initially established.

8.1 Literature Cited

Biging, G.S., and M. Dobbertin. 1992. A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. For.Sci. 38:695-720.

Biging, G.S., and M. Dobbertin. 1995. Evaluation of competition indices in individual tree growth models. For.Sci. 41:360-377.

Burton, P.J. 1993. Some limitations inherent to static indices of plant competition. Can.J.For.Res. 23:2141-2152

Cooke, B.J., and J. Roland. 2007. Trembling aspen responses to drought and defoliation by forest tent caterpillar and reconstruction of recent outbreaks in Ontario. Can.J.For.Res. 37:1586-1598.

Hogg, E.H., J.P. Brandt, and B. Kochtubajda. 2005. Factors affecting interannual variation in growth of western Canadian aspen forests during 1951-2000. Can.J.For.Res. 35:610-622.

Hogg, E.H., and R.W. Wein. 2005. Impacts of drought on forest growth and regeneration following fire in southwestern Yukon, Canada. Can.J.For.Res. 35:2141-2150.

Holmes, M.J., and D.D. Reed. 1991. Competition indices for mixed species northern hardwoods. For.Sci. 37:1338-1349

Kent, B.M., and P. Dress. 1979. On the convergence of forest stand spatial pattern over time: the case of random initial spatial pattern. For.Sci. 25:445-451.

Kent, B.M., and P. Dress. 1980. On the convergence of forest stand spatial pattern over time: the case of regular and aggregated initial spatial patterns. For.Sci. 26:10-22.

Leps, J., and Kindlmann, P. 1987. Models of the development of spatial pattern of an even-aged plant population over time. Ecol.Mod. 39:45-57.

Lorimer, C.G. 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. For.Ecol.Man. 6:343-360

Morris, D.M., and R.R. Forslund. 1992. The relative importance of competition, microsite, and climate in controlling the stem taper and profile shape in jack pine. Can.J.For.Res. 22:1999-2003.

Muirhawe, C.K., V.M. LeMay, and A. Kozak. 1994. Effects of adding tree, stand, and site variables to Kozak's variable-exponent taper equation. Can.J.For.Res. 24:252-259.

Oliver, C.D., and B.C. Larson. 1996. Forest Stand Dynamics. Update Edition. John Wiley and Sons, NY.

Schwinning, S, and J. Weiner. 1998. Mechanisms determining the degree of size symmetry in competition among plants. Oecologia 113:447-455

Sharma, M., and S.Y. Zhang. 2004. Height-diameter models using stand characteristics for *Pinus banksiana* and *Picea mariana*. Scand.J.For.Res. 19:442-451.

Tome, M., and H. Burkhardt. 1989. Distance-dependent competition measures for predicting growth of individual trees. For.Sci. 35:816-831.

van Niejenhuis, A., and W.H. Parker. 1996. Adaptive variation in jack pine from north central Ontario as determined by short-term common garden tests. Can.J.For.Res. 26:2006-2014

Weiner, J., and S.C. Thomas. 1986. Size variability and competition in plant monocultures. Oikos 47:211-222.

Wichmann, L. 2001. Annual variations in competition symmetry in even-aged sitka spruce. Ann.Bot. 88:145-151.